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Interactions between a root hemiparasite and 27 different hosts: growth, biomass allocation and plant architecture

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Abstract

The aim of this study was to investigate the effect of many different host species and their traits on the performance, morphology and architecture of the root hemiparasite *Melampyrum arvense* L., as well as the effect of the parasite on the growth and biomass allocation of its hosts. *M. arvense* was grown at two nutrient levels with 27 host species (grasses, legumes, and forbs) from habitats differing in nutrient availability. The biomass of the parasite varied enormously (475-fold) depending on the host species. The mean fraction of parasite biomass allocated to roots (RMF) decreased with increasing quality of a host (measured as total biomass of the parasite) and was only 3% with the best host. An extensive review of published studies showed that access to a host in most cases reduces RMF of root hemiparasites and that the RMF of annual root hemiparasites is low compared to that of autotrophic plants, suggesting that a reduced expenditure on roots is an important advantage of hemiparasitism for annual parasites. In contrast, the RMF of hemiparasitic perennial herbs and woody plants was found to be similar to that of autotrophic plants.

Host identity and nutrients also strongly influenced traits of *M. arvense* other than biomass, e.g. leaf size, seed mass, leaf chlorophyll concentration, nitrogen concentration, height, and the number of vegetative internodes. However, while host plant identity influenced allometric relationships, most of the effects of nutrient level were due to simple changes in overall parasite size. Individual parasite biomass was not correlated with the final shoot or root mass of the host plants growing in the same pot, but increased weakly with host nitrogen concentration. Mean host size at the time of parasite planting, host functional type and the nutrient state of the typical host habitat influenced mean parasite biomass and together explained 64% of its variation. Parasite growth increased with initial host mass, was higher with legumes and forbs than with grasses, and higher with hosts from nutrient-rich habitats.

Host damage due to parasitism increased with mean biomass of the parasite, and was lower for fast-growing species and higher for legumes and forbs than for grasses. Differences in damage between similarly good hosts indicated that not only resistance but also tolerance may be important for host responses to parasitism. *M. arvense* also caused changes in host allometry and increased host RMF, particularly in good host species. However, an extensive literature review found that there is no consistent general pattern of a higher RMF in hosts that are parasitized. Total productivity per pot was reduced by parasite presence suggesting lower resource use efficiency of the parasite, but not for all parasite - host combinations. Patterns of host quality for *M. arvense* and for its impact on host species differed strongly from those

found for the related model hemiparasite *Rhinanthus* and suggest that hemiparasite - host species interactions may be parasite-specific.

Keywords: Nitrogen concentration; biomass allocation; root mass fraction; parasite tolerance

1. Introduction

More than 1% of angiosperm species (4500 species, Heide-Jørgensen, 2013) are parasitic on other plants. Most parasitic plants are root hemiparasites that have green leaves and are capable of photosynthesis, but attack the roots of their host species with special contact organs (haustoria) and extract water, nutrients and assimilates (Cameron and Phoenix, 2013; Phoenix and Press, 2005a). In spite of their own photosynthesis, hemiparasites may derive a substantial part of their carbon from their hosts (Press et al., 1987; 1988; Tešitel et al., 2010).

Root hemiparasites mostly have a wide host range, but different plant species vary in their suitability as hosts (De Hullu, 1984; Guo and Luo, 2010; Hautier et al., 2010; Matthies, 1996; 1997; Schädler et al., 2005; Snogerup, 1982). The differences in the performance of hemiparasites have been related to various traits of their hosts. Many studies have found differences among functional groups of plants (legumes, grasses and non-leguminous forbs) in their suitability as hosts for hemiparasites. Legumes have often been found to be particular good hosts (e.g. Matthies, 1996; Seel et al., 1993), but there are some notable exceptions (Govier, 1966; Matthies, 1997). The particularly strong growth of hemiparasites with leguminous hosts has been attributed to their high nitrogen content (Phoenix and Press, 2005b; Seel et al., 1993) and weak defences against haustorial attack (Cameron et al., 2006). Grasses are assumed to be generally better hosts than forbs, because the roots of forbs have been found to be more strongly defended against the intrusion of haustoria (Cameron et al., 2006; Cameron and Seel, 2007).

It has also been suggested that fast growing species are better hosts than slow growing species because they will provide the parasites with more nutrients (Knutson, 1979). Similarly, Hautier et al. (2010) developed a model of host - hemiparasite interactions which predicts that the growth rate of parasites is strongly coupled to host growth rate and validated this prediction in an experiment in which the hemiparasite *Rhinanthus alectorolophus* was grown with nine grass species. De Hullu (1984) suggested that plants from nutrient-rich habitats should be better hosts than those from nutrient-poor habitats. However, most of the studies relating the performance of hemiparasites to host traits suffered from the fact that they

compared relatively few species of hosts and could therefore not formally test possible relationships (Pennings and Simpson, 2008).

The suitability of individual species as hosts for root hemiparasites has also sometimes been inferred from field studies that investigated with which species the parasites formed haustorial connections (Gibson and Watkinson, 1989; Suetsugu et al., 2012; Weber, 1976). However, the existence of haustoria attached to the roots of a plant does not mean that these haustoria are functional, because the host plants may block them (Cameron and Seel, 2007; Govier, 1966; Rümer et al., 2007). Only experimental studies can therefore show that a species is a suitable host for a parasite. Moreover, because hemiparasites have their own photosynthesis, the suitability of a species as a host may also be influenced by competition for light between hemiparasites and their host plants. For example, in an experiment with *Medicago sativa* as host, light competition by the host reduced the biomass of the hemiparasite *Odontites rubra* by 31% and that of *Rhinanthus serotinus* by 34% (Matthies, 1995a). The net effect of the presence of a host for a hemiparasite consists therefore of the positive effects of water and solutes taken up from the host roots and the negative effect of shading by the shoot and leaves of the host (Atsatt and Strong, 1970; Matthies, 1995a).

Because of the double role of hosts as suppliers of water and solutes as well as competitors for light, the relationship between hemiparasites and their hosts can be strongly influenced by nutrient availability (Matthies and Egli, 1999). Hemiparasites strongly compete with the host shoots for the resources taken up by the host roots, but are relatively weak competitors for light (Matthies, 1995a; Tešitel et al., 2015). Higher nutrient availability may reduce the negative effects of the parasites on their hosts and increase the impact of light competition by the hosts on the hemiparasites, which may be responsible for restricting root hemiparasites to relatively nutrient-poor habitats (Matthies, 1995a; Tešitel et al., 2013; 2014).

The identity of the host species may not only influence the biomass of hemiparasites, but also their patterns of biomass allocation, their morphology and architecture (Matthies, 1995a; b; 1997; 1998; Seel and Press, 1993; Snogerup, 1982). However, most studies did not investigate whether the observed effects were due to differences in allometric relationships or simple consequences of differences in parasite size. The plastic responses of hemiparasite traits to host species may contribute to the strong morphological variability among populations of root hemiparasites in the field, which is often attributed to genetic differences and used to delimit taxonomic units, but rarely confirmed experimentally (Jonstrup et al., 2016; Pleines et al., 2013).

Root hemiparasites may strongly reduce the growth of their host species (Joshi et al., 2000; Matthies and Egli, 1999; Mizianty, 1975). Hemiparasites of the genus *Striga* are important agricultural weeds in tropical agricultural systems that cause great losses in grain yields (Parker, 2013), and *Melampyrum arvense* was formerly a noxious weed of cereal crops in Europe (Benkov, 1978). The negative impact of even very small plants of *Striga* on their hosts is so strong that it has been suggested that toxins may be involved (Ransom et al., 1996; Shen et al., 2006). However, the impact of other root hemiparasites on their hosts is less severe and may be explained by the loss of water, nutrients and carbon to the parasites. If a source – sink relationship is sufficient to explain the negative effects of a hemiparasite on its hosts, the strength of the negative impact of the parasite on the growth of a host species should increase with the benefits the host provides to the parasite, i.e. with parasite biomass (Knutson, 1979). There is evidence that good hosts suffer more from parasitisation than poor hosts from studies comparing the growth of parasites with a few host species (Atsatt and Strong, 1970; Matthies, 1996), but the suggested relationship has not been formally tested using a large number of hosts.

The combined productivity of hemiparasites and their hosts is often lower than that of the hosts grown without the parasite, indicating that the loss of host biomass due to parasitisation is not compensated by the biomass production of the parasite (Ameloot et al., 2005; Hautier et al., 2010; Matthies, 1997; Phoenix and Press, 2005a). The model of Hautier et al. (2010) even predicts that the combined bomass of hemiparasites and their hosts will always be lower than that of the host grown alone. The overall loss of productivity due to parasitism has been attributed to a lower efficiency of resource use by the parasite (Matthies, 1995a). Hemiparasites have much higher transpiration rates than their hosts which they keep up even at night (Press et al., 1988). Negative effects of parasitisation on host photosynthesis have also been found and may contribute to the reduced productivity (Cameron et al., 2008; Watling and Press, 2001). Because of their negative effect on biomass production, it has been suggested to use root hemiparasites as a conservation management tool to reduce the productivity of grassland communities in nature reserves and thus to potentially increase diversity (Westbury et al., 2008). However, significant impacts of hemiparasites on overall productivity of grasslands have not been consistently found in experimental studies (Hellström et al., 2011).

In addition to reductions in host biomass, hemiparasites may also induce changes in host morphology, architecture and, in particular, biomass allocation (Graves, 1995; Matthies, 1997; Press et al., 1999). However, the effects of parasitisation on biomass allocation has been

studied only in few hemiparasite - host associations. Frequently, parasitism resulted in higher allocation to roots by the hosts (Graves, 1995; Gurney et al., 2002; Matthies, 1997), but this effect was not universal (Li et al., 2012a; Matthies, 1995a; 1997).

I studied experimentally the effect of 27 different host species on the performance, morphology and architecture of the root hemiparasite *Melampyrum arvense* L. and the effect of the parasite on the growth and biomass allocation of its host plants. In Central Europe, *M. arvense* was formerly a common weed of cereal fields, but today is restricted mainly to two types of habitats: nutrient-poor calcareous grasslands and somewhat more nutrient-rich grasslands at waysides. Parasites growing in the more nutrient-rich wayside habitats attain a much larger size than those in nutrient-poor grasslands. However, the two types of habitat do not only differ in nutrient status, but also strongly in the potential host species available (Matthies, 1986; 1991). To study the effect of host traits on the size, morphology and other traits of *M. arvense*, the parasite was grown with species that represent different functional groups (grasses, legumes and non-leguminous forbs) and grow in habitats of different nutrient availability. Parasite performance was then related to various host traits like relative growth rate, initial size, final size and nitrogen content, as well as host functional group and habitat. To study the effects of nutrient availability on the relationship between *M. arvense* and its host plants, all parasite-host combinations were grown at two nutrient levels.

2. Material and methods

2.1. Study species

Melampyrum arvense (Orobanchaceae, previously included in the Scrophulariaceae) is an annual root hemiparasite. Seeds of *M. arvense* germinate in autumn and winter at low temperatures, but only the roots develop during winter, while the epicotyl stays dormant (Oesau, 1973). The cotyledons emerge in early spring (March – April) and the plant develops quickly. Plants start to flower in May – June. The flowers are pollinated by bumblebees (Kwak, 1988). *M. arvense* produces large seeds that resemble those of cereals with which they were in former times harvested and sown. Short-distance dispersal is by ants which are attracted by an elaiosome.

M. arvense was formerly a common weed of rye and wheat fields in central and eastern Europe, but due to the purification of crop seeds and the intensification of agriculture the species has become rare and is now threatened in many parts of Europe (Cheffings and Farrell, 2005; Garve, 1993; Hulina, 2005; Rassi et al., 2010; Sparrius et al., 2014; Woff-

Straub et al., 1999). However, in the 20th century it has become restricted to calcareous grasslands and waysides on limestone with an *Arrhenatheretum* type of vegetation (Matthies, 1986; 1991).

2.2. Experimental set-up

The hemiparasite *M. arvense* was grown in a factorial design with 27 host species at two nutrient levels. Seeds of *M. arvense* had been collected in a population near Göttingen, Germany, while seeds of the hosts had either been obtained from a commercial supplier or been collected near Zürich, Switzerland. All species used as hosts in the experiment are known to occur together with *M. arvense* in Central Europe (Matthies, 1991). The host species were further selected to include species from habitats with different nutrient availability. According to its indicator value for nutrients (N-value, Ellenberg et al., 1992) each species was assigned to one of three groups (Table 1): Species typical for low-nutrient habitats (N-value 2 or 3), for moderately nutrient-rich habitats (N-value 4 - 6), and for nutrient-rich habitats (N-value 7 or 8). Species that were not classified as characteristic for a certain nutrient level by Ellenberg et al. (1992) were assigned to the intermediate group. No indicator value was also available for wheat (*Triticum aestivum*), which was assigned to the high nutrient group, as modern crop plants are bred to utilize high amounts of nutrients. Within each group, species from three functional groups were included: grasses, legumes and non-leguminous forbs.

Seeds of *M. arvense* were sown in mid February on moist filter paper in Petri dishes and kept in a fridge at 5 ^{o}C until cotyledons were produced. Seeds of the host plants were sown in mid March on moist filter paper in Petri dishes at 20 ^{o}C in the laboratory. In early April, seedlings of each host plant were transplanted into 35 pots (8 cm diameter) filled with nutrient-poor commercial potting soil (NPK each 150 mg L^{-1}, pH 5.8). Into each pot two seedlings of a host species were planted c. 5 cm apart. The pots were kept in flower beds on gravel in the experimental garden of the Department of Evolutionary Biology and Environmental Studies, University of Zurich.

In mid May, after six weeks of growth, the plants in five pots per species were harvested above ground, dried at 80 ^{o}C for 48 h and weighed to obtain a measure of host size at the beginning of the experiment. The other plants were used for the main experiment. One seedling of the parasite *M. arvense* was transplanted into the center of 20 replicate pots for each host species. Only parasites whose cotyledons had already developed were used. The remaining 10 replicate pots for each host species served as controls to study the effect of *M.*

arvense on the hosts. Parasites and hosts were initially grown in small pots to facilitate the contact between parasite and host roots and thus haustoria formation. Parasites that died were replaced during the first two weeks of the experiment, but not afterwards.

Half of the pots for each host species (high nutrient treatment) received 60 ml of a nutrient solution prepared with a commercial fertilizer (Wuxal, Syngenta, Switzerland) containing 400 mg N L^{-1}, 400 mg P_2O_5 L^{-1} and 300 mg K_2O L^{-1}. The other pots received the same amount of water (low nutrient treatment). To prevent contamination with fertilizer all pots were placed on saucers. To maintain the differences between the nutrient treatments, the high nutrient plants received another 60 ml of the same nutrient solution three weeks and six weeks after planting of the parasites.

The plants were watered as necessary and randomized within and between flower beds every two weeks. To prevent water-logging, the plants were protected against rain during thunderstorms and longer periods of rain by transparent foil tunnels. Eight weeks after the planting of the parasites, the intact soil cores with the plants were transplanted into larger pots of 15 cm diameter filled with the same type of soil. The high nutrient plants received another 60 ml of the nutrient solution.

Once the parasites had started flowering, they were checked daily for ripe seeds. These were collected, dried for three months at room temperature, counted and weighed. Mean individual seed mass was calculated for each parasite that had produced seeds. When the parasites had grown for 17 weeks with the hosts the following traits were measured for each parasite: Stem height, stem diameter just above ground level, length and width of the longest leaf, number of leaves, total length of all branches, number of nodes below the first flower, length of the main inflorescence, number of flowers along the main inflorescence, and total length of all inflorescences. In addition, the chlorophyll content of leaves was measured using a portable chlorophyll meter (SPAD-502, Minolta). Three readings per plant were taken and averaged. The values measured by the instrument are related by a second order polynomial to the actual chlorophyll content of a leaf (Richardson et al., 2002) and I calculated chlorophyll content values using the equation for total chlorophyll content given by Richardson et al. (2002).

After the measurements, hosts and parasite were harvested separately above ground, dried at 80 ^{o}C for 48 h and weighed. To study the variation between the two host individuals within each pot, they were weighed separately, but separating the two individuals was not possible in the case of *Trifolium repens.* As a measure of variation, coefficients of variation (CV) were calculated for the two host individuals. For each of the host species its relative growth rate

(RGR) without the parasite was calculated as log (mean shoot mass after 23 weeks / mean shoot mass after six weeks of growth).

The pots containing the soil and the roots were dried at 60 ^{o}C for 48 h to prevent decomposition and stored in a dry place for later analysis. In the laboratory, after soaking in water for a few hours, the soil was removed carefully from the roots by washing and the roots of parasites and hosts were separated, dried and weighed. The roots of the two host individuals could not be separated. The shoots of the parasites and the hosts were milled and element concentrations were determined with a CHN-analyzer (Leco, St. Joseph, MI, USA).

2.3. Statistical analyses

The effects of host species and nutrient level on parasite traits were assessed using two-way ANOVAs. To analyse whether host species and nutrient levels had effects on traits of the parasite that could not be explained by effects on parasite size (biomass), the effects of host species and nutrients on various parasite traits were analysed with general linear models that included parasite biomass as an explanatory variable in addition to host species and nutrient level. Significant effects of host species or nutrient level on traits in these models indicate effects of the factors on allometric relationships between traits and biomass (Warton et al. 2006). To illustrate the differences between trait values of parasites of the same size grown with different host species, predicted values for these traits were calculated for parasites of 1 g biomass. Non-significant terms were removed from the predictive equations, except if they were part of significant higher order interactions. Values are only presented for parasite - host combinations for which at least one parasite in the experiment produced a biomass of more than 1 g.

The influence of host species and nutrient level on parasite survival was assessed using chi^2-tests. The relationship between the probability of flowering of a parasite individual and its biomass was analysed by logistic regression. The relationship between biomass of parasite individuals and characteristics of the host individuals growing in the same pot were analysed by linear regressions. Differences in the N-content of parasites and hosts growing in the same pot were assessed with paired t-tests.

The influence of various traits of the host species on parasite growth was analysed by regressions between mean parasite biomass and the following host traits, measured for hosts grown without the parasite: mean initial host size, mean relative growth rate of the hosts, mean final host biomass, host nitrogen content, and C/N-ratio of the host. Moreover, the effects of host functional group (grass, legume or forb) and typical nutrient status of the host

habitat (nutrient-poor, moderately nutrient-rich, nutrient-rich) were analysed by one-way analyses of variance. The amount of variation in parasite biomass explained by the variables and factors was expressed as r^2. To analyse the simultaneous effects of the various host traits on parasite growth, mean parasite biomass was related to all the various host traits in a general linear model. A minimum adaequate model was then obtained by backward elimination of non-significant effects (Crawley 2013). Unique contributions of the variables to variation in parasite biomass were then determined by hierarchical partitioning (Chevan and Sutherland, 1991).

Effects of the host species, nutrient level and the presence of the parasite *M. arvense* on various host traits and the total biomass per pot (hosts + parasite) were assessed by three-way ANOVAs. Relationships between the mean damage to the host by the parasite, measured as the relative reduction in biomass compared to that of hosts grown without the parasite, and the mean biomass of the parasite were studied by linear regression. The influence of mean initial size of the hosts and RGR of the hosts grown without the parasite on parasite biomass was analysed by linear regression, and the effects of host functional group and nutrient status of the host habitat by one-way ANOVAs. The simultaneous effects of these variables on parasite size were assessed by a general linear model. A minimum adaequate model was then obtained by backward elimination of non-significant effects.

Effects of host species, nutrient level and the presence of the parasite on the proportion of biomass allocated by the host species to their roots (root mass fraction, RMF) were assessed by three-way ANOVA. In addition, effects of the three factors on biomass allocation to roots were also analysed in a general linear model relating log shoot mass of the hosts to log root mass, the three factors of interest, and their interactions.

To achieve normally distributed residuals and homoscedasticity, data for several variables were log-transformed prior to analysis. Data were analysed by IBM-SPSS 22. Hierarchical partitioning was performed using the hier.part package of the R statistical language (Walsh and Mac Nally, 2003).

3. Results

3.1. Effects of the experimental treatments on parasite growth

There was some mortality among the parasites, mostly in the first weeks after they had been transplanted. However, mortality of the parasites was not significantly influenced by host species ($Chi^2 = 29.6$, df = 26, p = 0.28) or nutrient availability ($Chi^2 = 1.10$, df = 1, p = 0.30).

The biomass of the parasites varied enormously depending on the host species (Tab. 2, Fig.1). The shoot mass of *M. arvense* grown with the best host (*Medicago sativa*) at the low nutrient level was 171 times and that grown at high nutrients 475 times the shoot mass of parasites grown with the worst host (*Trisetum flavescens*, Fig. 1a). At high nutrient levels parasite biomass was on average 35% higher than at low nutrient levels. The effect of nutrients depended to some extent on the host species, but this interaction effect was small compared to that of the host species and nutrient level. The root mass of the parasites was also strongly influenced by host species and was on average higher at higher nutrient availability (+21%), but root mass depended to some extent on the specific combination of host and nutrient treatment (Fig. 1b).

Access to a good host increased shoot mass of the parasites far more than root mass. In consequence, the proportion of biomass allocated by the parasites to their roots (root mass fraction, RMF) strongly differed depending on the host species (Table 2) and decreased with parasite mass, i.e. host quality (Fig. 2). The RMF of parasites grown with the worst host *T. flavescens* was 25%, whereas grown with the best host *Medicago sativa* the parasite invested only 3% of its biomass into roots. In contrast, parasite RMF was little influenced by nutrient level. High nutrient levels reduced mean RMF of the parasites slightly from 12% to 11%.

3.2. Treatment effects on other traits

The different host species not only strongly influenced the shoot and root mass of the parasites, but also all other parasite traits measured (Tables 2 and 3), including morphological as well as physiological traits. The strongest variation was shown by traits directly related to the size of the plants like total branch length, inflorescence length and number of leaves. Most of the traits were also affected by nutrient level and its interaction with host identity, but their effects were usually much smaller, with the exception of the effects of nutrient level on mean seed mass, inflorescence length and leaf chlorophyll content. Traits that relate to the size of individual plant parts like leaf length and width were not influenced by nutrient level, but were strongly influenced by host identity. The number of vegetative nodes below the inflorescence was also influenced by host species.

Reproduction is of particular importance for an annual plant like *M. arvense*. The probability of the parasites developing flowers increased with their size (Fig. 3), with a threshold size of c. 35 mg. While only 5% of the parasites with a biomass of less than 35 mg flowered, 90% of those with more than 90 mg did. Because of their effect on parasite size, the different hosts also influenced the reproductive behaviour of the parasite. Less than 50% of the *M. arvense*

plants grown with *Koeleria*, *Papaver*, *Anthyllis*, *Cynosurus*, *Dactylis*, and *Bromus* flowered, and those that flowered did not produce seeds. Parasite grown with *Trisetum* did not even produce flowers. Both the length of the inflorescences, which was a good predictor of flower number ($r = 0.97$, $n = 282$), and seed mass were strongly influenced by the host species. Mean seed mass varied from only 9.1 mg for parasites grown with *Myosotis* to 20.7 mg for those grown with *Medicago lupulina*. Higher nutrient levels increased mean seed size slightly by on average 1.71 mg.

The nitrogen content of *M. arvense* varied depending on the host species from 0.84% with *Cynosurus cristatus* to 3.62% with the legume *Medicago sativa* (Tables 2 and 3). Parasites growing with legumes as hosts had generally higher nitrogen concentrations (mean 2.29%; $F_{2,24} = 20.1$, $p < 0.001$) than those growing with other forbs (1.13%) or grasses (1.05%). An exception were parasites growing with *Anthyllis vulneraria* (N-content only 1.17%). Higher nutrient levels had no consistent effect on parasite nitrogen content. With most host species parasite nitrogen content increased with nutrient level, but with some hosts it was reduced. This was mostly the case with poor hosts like *Festuca*, *Trisetum*, *Koeleria* and *Anthyllis*, but also with some good hosts like *Medicago sativa* and *Trifolium repens*.

Nitrogen concentrations of the parasite were higher than those of the hosts for parasites grown with most of the host species (Fig. 4). Much higher nitrogen concentrations of the parasites than of their hosts were found for parasites grown with the very good host *Medicago sativa* (+108% higher in parasites), the poor host *Plantago lanceolata* (+94%) and the very poor host *Papaver rhoeas* (+67%). In contrast, nitrogen concentrations of the parasites were lower than those of their hosts for some parasites grown with hosts of poor quality like *Anthyllis vulneraria* (-48%) and *Myosotis arvensis* (-40%). Leaf chlorophyll content of the individual parasites was correlated with shoot nitrogen content ($r = 0.67$, $p < 0.001$) and varied strongly depending on host species (Table 3). Higher nutrient levels increased leaf chlorophyll concentration with all host species by a similar degree (+13%).

3.3. Treatment effects corrected for size

All parasite traits studied were significantly influenced by parasite size (Table 4). Variation in biomass explained 5% of the variation in seed mass, 15% of that in nitrogen content (Fig. 5a), 63% of that in chlorophyll content (Fig. 5b) and more than 70% of the variation in the other traits. Similarly, variation in parasite shoot mass explained 90% of the variation in root mass. To test whether the different host plants and nutrient availability had an influence on parasite traits that could not be explained by their effects on parasite size, their effects were adjusted

for parasite size by including parasite biomass (or shoot mass) as a covariate in the analyses (Table 4). Effects of host identity on all traits remained highly significant after adjusting for plant size, indicating that the host plants influenced allometric relationships. In contrast to host species identity, nutrient level did not have significant effects on most parasite traits if adjusted for plant size, with the exception of the two physiological traits chlorophyll and nitrogen content, and the morphological traits leaf number and branch length (Table 4). This indicates that most of the effects of nutrient level on morphological traits of the parasite were just due to changes in overall plant size.

Because the different hosts changed allometric relationships of the parasite, they influenced the allocation patterns, morphology and architecture of *M. arvense*. Thus, parasites of the same shoot mass, but grown with different host species, invested different amounts of biomass into their roots. For instance, the mean root mass of parasites of 1 g of shoot mass grown with *Urtica dioica* as a host at high nutrients was 30 mg, while that of parasites grown with *Arrhenatherum elatius* was 99 mg (Fig. 6a). Similarly, parasites of the same total biomass, but grown with different hosts, differed in morphological and physiological traits (Fig. 6b-h). For example, parasites of 1 g biomass grown with *Chrysanthemum leucanthemum* as hosts were on average 26 cm high, while those grown with *Matricaria chamomilla* were 34 cm high (Fig. 6b); parasites of 1 g grown with *Medicago sativa* at high nutrient levels produced 91 leaves, while those grown with *Arrhenatherum elatius* produced only 58 leaves (Fig. 6c), and parasites of 1 g grown with *Trifolium repens* had a total branch length of 94 cm while those grown with *Medicago lupulina* had only one of 42 cm (Fig. 6d).

The host species also affected the two reproductive traits inflorescence length and seed mass of the parasites. Parasites of 1 g of biomass grown with *Medicago lupulina* as host produced an inflorescence of 9 cm length, while those of the same biomass grown with *Medicago sativa* produced one of 20 cm (Fig. 6e). The mean mass of seeds of parasites of 1 g biomass grown with *Medicago sativa* was 12 mg, while that of parasites grown with *Lotus corniculatus* was 20 mg (Fig. 6f).

Chlorophyll content of the leaves of parasites of 1 g grown with *Capsella* at high nutrients was 18 µg cm^{-2}, while that of parasites grown with *Lotus* and *Trifolium pratense* was 45 µg cm^{-2} (Fig. 6g). The nitrogen content of *M. arvense* plants of 1 g of biomass varied from 0.98% for parasites grown with *Chrysanthemum leucanthemum* at high nutrient levels to 3.3% for those grown with *Medicago sativa* (Fig. 6h)

3.4. Determinants of host quality

Individual parasite biomass was not correlated with either the final shoot mass ($r = 0.004$, $F_{1,383} = 0.006$, $p = 0.94$), or the final root mass ($r = 0.06$, $F_{1,383} = 1.44$, $p = 0.23$) of the host plants growing in the same pot. The biomass of individual parasites increased significantly with the nitrogen content of their individual hosts ($r^2 = 0.022$, $F_{1,383} = 8.43$, $p = 0.004$) and decreased with their C/N-ratio ($r^2 = 0.026$, $F_{1,383} = 10.04$, $p = 0.002$), but the relationships were very weak. The effect of both host nitrogen content ($r^2 = 0.051$) and C/N-ratio ($r^2 = 0.052$) were stronger if parasites grown with *Anthyllis* were omitted.

At the species level, of the traits considered initial host size ($r^2 = 0.21$, $F_{1,25} = 6.55$, $p < 0.05$) significantly increased parasite biomass, whereas the effects of host functional group ($r^2 = 0.16$, $p = 0.12$) and nutrient status of host habitat ($r^2 = 0.16$, $p = 0.13$), and RGR of the hosts ($r^2 = 0.01$, $p = 0.58$), final host biomass ($r^2 = 0.06$, $p = 0.21$), host nitrogen content when grown without the parasite ($r^2 = 0.05$, $p = 0.26$) and C/N-ratio of the hosts ($r^2 =0.07$, $p = 0.18$) were not significant. However, omitting parasites grown with the unsuitable legume *Anthyllis vulneraria* considerably increased the effects of host nitrogen content ($r^2 = 0.15$, $p = 0.05$; positive effect) and host functional group ($r^2 = 0.24$, $p < 0.05$).

The combined effect of the various host traits on mean parasite biomass was analysed with general linear models. In a minimum adequate model the effects of host size at the time of parasite planting ($F_{1,21} = 11.52$, $p < 0.001$), host functional group ($F_{2,21} = 10.50$, $p < 0.01$) and the nutrient state of the host habitat ($F_{2,21} = 4.37$, $p < 0.05$) had a significant effect on parasite biomass and together explained 64% of its variation. Hierarchical partitioning of the effects of these host traits showed that the unique effect of initial host size accounted for 20% of the variation in parasite biomass, that of host functional group for 29% and that of host habitat type for 15%. Parasite mass increased with the initial size of the host, indicating a positive effect of the capacity of a host to provide resources for the parasite (Fig. 7). For each increase of 221 mg in initial host biomass, final parasite biomass doubled. Grasses were worse hosts for the parasites than forbs and legumes (Fig. 8a). Adjusted for the effects of initial host biomass, the shoot mass of the parasite grown with a forb as host was on average 3.9 and that of parasites grown with a legume 11.7 times that of parasites grown with a grass. Plant species from high-nutrient habitats were much better hosts than species typical for moderately nutrient-rich or low-nutrient habitats (Fig. 8b).

3.5. Effects of the parasite M. arvense *and nutrient level on the host plants*

The biomass of the hosts varied strongly between species and was higher at high nutrient levels (Table 5). The presence of the parasite *M. arvense* generally reduced host biomass (mean: -22%). The damage to host growth varied strongly among species, but was hardly influenced by nutrient level. While the biomass of some poor hosts like *Trisetum flavescens*, *Koeleria pyramidata* and *Festuca ovina* was not affected by parasitism, the biomass of other species like *Capsella bursa-pastoris* (-70%) and *Medicago sativa* (-65%) was strongly reduced. The damage to a host species increased with mean parasite biomass, i.e. the more suitable a species was as a host for *M. arvense*, the more it was damaged by the parasite and its biomass reduced (Fig. 9). However, the response of some species deviated strongly from the general trend. *Capsella bursa-pastoris* was more strongly damaged by the parasite, while *Trifolium pratense*, *Arrhenatherum elatius* and *Lotus corniculatus* were less affected than would be expected from the general relationship between host damage and parasite benefit. In single analyses of the effects of various traits of the hosts on their degree of damage due to the parasite only their functional group had a certain effect on the degree of damage by the parasite ($F_{2,24} = 3.16$, $p = 0.06$). In a multiple regression analysis, only host functional group ($F_{2,23} = 4.78$; $p < 0.05$) and the RGR of the hosts when grown without the parasite ($F_{1,23} = 4.74$; $p < 0.05$) remained in the minimum adequate model, while the mean initial size of hosts and the nutrient status of their habitats had no effect. Damage by the parasite decreased with the RGR of the host plants (beta = -0.47). Adjusted for differences in RGR, the mean biomass of legumes was reduced by the parasite by 33.3%, that of forbs by 28.3%, and that of grasses by only 5.8%.

The presence of the parasite increased the coefficient of variation of shoot mass of the two host individuals in a pot from 0.37 to 0.46, indicating that one of the two individuals in a pot suffered somewhat more than the other from parasitisation. This effect of parasitisation on host size variability was similar for all host species (Table 5).

The proportion of biomass allocated by the host plants to their roots (root mass fraction, RMF) varied strongly among species and was lowest for annuals like *Myosotis arvensis*, *Capsella bursa-pastoris* and *Matricaria chamomilla* (Fig. 10). The presence of the parasite influenced the RMF of the hosts, but the effect varied among species (Table 5). Most host species increased their relative allocation to roots in response to parasitisation (Fig. 10). This was most pronounced in *Medicago lupulina* (increase in RMF from 0.27 to 0.36), *Capsella bursa-pastoris* (from 0.12 to 0.20), and *Plantago lanceolata* (from 0.33 to 0.41). In contrast, small reductions in RMF were observed for some of the very poor hosts like *Koeleria*

pyramidata, *Trisetum flavescens* and *Cynosurus cristatus*. The increase in RMF in response to the presence of the parasite was on average much stronger in forbs (+0.037) and legumes (+0.042) than in grasses (-0.007; $F_{2,24} = 7.3$, $P < 0.01$), and increased with the mean biomass of the parasite ($r = 0.42$, $p < 0.05$), i.e. good hosts changed their biomass allocation more strongly than poor hosts. The effect of the parasite on the RMF of the host species depended also on nutrient level (Table 5). At low nutrients, the parasite increased the mean RMF of the host species from 0.37 to 0.38, while at high nutrients it increased it from 0.36 to 0.40. An allometric analysis of the influence of the parasite and nutrients on the relationship between log root mass and log shoot mass of the hosts confirmed these results: adjusted for host shoot mass, the presence of the parasite generally increased host root mass (parasite presence: $F_{1,465} = 6.6$; $p < 0.05$), but this effect varied among hosts (parasite x host: $F_{26, 465} = 1.6$; $p < 0.05$), and was stronger at high nutrient levels (parasite x nutrients: $F_{1,465} = 10.7$; $p < 0.01$). In contrast, the effect of the parasite on host root mass did not depend on host size (parasite x host shoot mass: $F_{1,465} = 0.89$; $p = 0.35$). The results of the allometric analysis thus show that the effects of the parasite on root allocation by the host were not merely the consequence of changes in host size, but due to changes in allometry.

Nitrogen content varied strongly among the different host species (from 0.55% in *Plantago* to 2.2% in *Anthyllis*) and was higher at high nutrient levels (Table 5). The N-content of legumes was higher than that of grasses and forbs, both for hosts grown without a parasite (1.91% vs. 1.06%; $F_{1,25} = 81.2$, $P < 0.001$) and for those grown with the parasite *M. arvense* (1.96% vs. 0.99%; $F_{1,25} = 97.4$, $P < 0.001$). The parasite reduced mean nitrogen content of the hosts slightly, but significantly, from 1.25% to 1.21%. This effect varied little among different hosts (Table 5).

The presence of the parasite *M. arvense* influenced total biomass production by the plants grown in a pot, i.e. the sum of parasite and host biomass (Table 5). Overall, productivity was reduced by the parasite by 11.1%, indicating that the loss in biomass production of the hosts due to parasitisation was on average not fully compensated by the biomass production of the parasite, resulting in reduced productivity. However, the effect of the parasite on overall productivity varied depending on the particular combination of host species and nutrient level (Fig. 11). While with most species the effect of the parasite on total productivity was similar at both nutrient levels, when grown with *Capsella bursa-pastoris*, *Medicago lupulina*, *Trifolium pratense* and *Taraxacum officinale* the parasite significantly reduced productivity at low nutrient levels, but increased it at high nutrient levels ($p < 0.05$ for the parasite x nutrient interaction in analyses separate by host species).

4. Discussion

4.1. Effects of different hosts on parasite growth

The quality of the 27 studied plant species as hosts for the hemiparasite *M. arvense* varied enormously. The biomass of parasites grown with the best host *Medicago sativa* was more than 400 times higher than that of parasites grown with the worst host *Trisetum flavescens*. However, the studied species cannot be simply divided into hosts and non-hosts, because there was a continuum in host quality for *M. arvense.* The survival of the parasites even with very poor hosts suggests that all host species provided at least some benefit for the parasite, as *M. arvense* is an obligate parasite and plants without a host cannot complete their life-cycle (Lechowski, 1995; Matthies, 1996; Oesau, 1973). However, for an annual species like *M. arvense* fitness depends solely on seed production and none of the parasites grown with one of the seven poorest hosts did produce any seeds. Plants of *M. arvense* grown with *Trisetum flavescens* did not even produce flowers.

The observed range in host benefit to the parasite *M. arvense* was much larger than that found in other studies in which root hemiparasites were grown with different host species (Atsatt and Strong, 1970; Calladine et al., 2000; Cameron et al., 2006; Cameron and Seel, 2007; Dalrymple, 2007; De Hullu, 1984; Gibson and Watkinson, 1991; Guo and Luo, 2010; Hautier et al., 2010; Lackney, 1981; Marvier, 1996; Matthies, 1995a; b; 1996; 1997; 1998; Pate and Bell, 2000; Radomiljac, 1998; Ren et al., 2010; Rowntree et al., 2014; Seel et al., 1993; Wilkins, 1963). One reason is probably the particularly large number of host species (27) from different families used in the present study which increased the probability that very poor and very good hosts were among the species investigated and thus the range in host quality. However, even in the few other studies that have used many host species, differences among species in host quality were much smaller. De Hullu (1984) grew the root hemiparasite *Rhinanthus angustifolius* with 18 host species and found a c. 20-fold variation in parasite biomass, Seel et al. (1993a) observed a 13-fold variation in the height of *Rhinanthus minor* grown with 11 host species, Calladine et al. (2000) found a 6-fold variation in biomass of the root hemiparasite *Nuytsia floribunda* (Loranthaceae) with 24 species of hosts, Rowntree et al. (2014) a 6-fold variation in the biomass of *R. minor* with nine hosts, Hautier et al. (2010) a 2.4-fold variation in the biomass of *Rhinanthus alectorolophus* grown with nine grass species, and Guo and Luo (2010) a 3.5-fold variation in the biomass of *Thesium chinense* (Santalaceae) with eight host species.

Another possible factor for the particularly large range in host quality found for *M. arvense* is the long period of time (17 weeks) the parasite was grown in the present experiment in comparison to other studies (e.g. Guo and Luo, 2010: 12 weeks; Hautier et al., 2010: 14 weeks; Rowntree et al., 2014: 16 weeks), which may have contributed to the greater accumulation of biomass with good hosts. Moreover, *M. arvense* is an obligate parasite that strongly depends on its host plants, which resulted in hardly any growth with poor host species. The final biomass of *M. arvense* grown with *Trisetum flavescens* was only 1.2 times that of the seed mass of the parasite.

The suitability of a species as a host for hemiparasites is known to be influenced by various traits (Cameron et al., 2006; Marvier and Smith, 1997). These include root architecture (Radomiljac, 1998) and thickness (Davies and Graves, 2000; Marvier, 1998a), nutrient content (Press et al., 1993; Seel et al., 1993), extent of shading of the parasite by the host shoot (Matthies, 1995a) and defence of the host roots against the invading haustorium (Cameron et al., 2006; Cameron and Seel, 2007; Govier, 1966; Rümer et al., 2007). In the current study the possible role of a number of factors as determinants of host quality for the parasite *M. arvense* was investigated. In a general linear model, the mean size of a host species at the time of planting of the parasite had the strongest influence on mean final biomass of the parasite *M. arvense*, followed by host functional group (legume, forb or grass) and the realized niche of the host with respect to nutrients, as indicated by its Ellenberg indicator value for nutrients. These host traits together explained 64% of the variation in mean parasite size. In contrast, several other traits had little or no influence. Host nitrogen content was significantly correlated with mean parasite biomass, but did not explain a significant part of the variation in parasite size in addition to the three traits mentioned. Host biomass at the end of the experiment and host relative growth rate had no effect, neither individually, nor in combination with other variables. The results thus do not support the prediction by the model of Hautier et al. (2010) that parasite biomass should be greater when growing on host species with higher growth rates.

It is likely that host plants whose shoot mass (initial size) was large when the parasites were planted next to them also had large root systems which may have facilitated a fast attachment of *M. arvense* to the host. Parasites that attach to a host earlier may strongly benefit from a longer period of heterotrophic growth (Keith et al., 2004; Svensson et al., 2001). Moreover, hosts with a large initial size may have provided the young parasites with more water, nutrients and carbon than small hosts (Seel and Press, 1996), resulting in higher photosynthesis and growth of the hemiparasite. However, a large host shoot can also be a

strong competitor for light (Matthies, 1995a) and for resources taken up by the root system of the host. The relationship between final host and parasite size will thus also be influenced by the negative effects of parasitism on the host. These conflicting interactions between hosts and parasites may have been responsible for the lack of a relationship between the final size of *M. arvense* plants and the biomass of its host plants.

Legumes, with the exception of *Anthyllis vulneraria,* were particularly good hosts for *M. arvense*, while grasses were on average rather poor hosts. Legumes and grasses are typical components of the habitats of root hemiparasites and have therefore been used in many experiments on parasite-host relationships. As in the current study, legumes were often found to be particular good hosts, although there were a number of exceptions (see references in Marvier and Smith, 1997; Dalrymple, 2007; Marvier, 1998a; Matthies, 1997; 1998; Radomiljac et al., 1998; Rowntree et al., 2014). The often observed particularly strong growth of hemiparasites with leguminous hosts has been attributed to the high nitrogen content of legumes and the lack of a defensive response of their roots to the invading haustorium (Cameron et al., 2006; Jiang et al., 2008; Rümer et al., 2007; but see Govier, 1966 for a defensive response of *Trifolium incarnatum* against *Odontites verna*). Overall, the results of the current study lend some support to the notion that nitrogen obtained from the hosts is of particular importance for hemiparasites (Penning and Simpson, 2008; Phoenix and Press, 2005a). Like in *Rhinanthus minor* (Seel and Press, 1993), in the present study mean N-concentrations were highest in parasites attached to a legume and the N-content of the parasites was usually higher than that of the hosts, except when grown with some poor hosts. The biomass of *M. arvense* increased with the N-content of the host individuals it was grown with, but the correlation was weak. However, the N-content of individual host plants may not be a good predictor of parasite growth, if vigorously growing parasites deplete the nutrient content of their hosts. At the species level, the biomass of *M. arvense* increased with the mean N-content of the host species grown without the parasite, but the correlation was also weak. However, the relationship improved considerably without parasites grown with *Anthyllis vulneraria*, which although a legume with a particularly high N-content is clearly an unsuitable host for *M. arvense*. An important role of nitrogen taken up from the host for parasite performance is also suggested by the close correlation between the biomass of the hemiparasites and their leaf chlorophyll concentration, because the chlorophyll concentration is correlated with leaf nitrogen content (Bonneville and Fyles, 2006; Chang and Robison, 2003; Radomiljac et al., 1999).

Phoenix and Press (2005b) have raised the question whether the performance of hemiparasites is better on N-rich hosts because they are a higher quality resource (low C:N ratio) or because they are a larger resource (greater N-content). Both traits were measured in the experiment with *M. arvense* and were weakly related to parasite biomass. However, it was not possible to compare the effect size of the two traits, because C:N ratio and N-content of the host plants were highly correlated (r = -0.91).

It has been suggested that grasses are generally good hosts for hemiparasites because they have a dense root system and their roots are only weakly defended against parasite attack (Cameron et al., 2006; Cameron and Seel, 2007), but grasses were on average poor hosts for *M. arvense*. This is in contrast to the results of a number of studies on *Rhinanthus* (Cameron et al., 2006; Cameron and Seel, 2007; Hautier et al., 2010; Keith et al., 2004). However, in these studies few host species were investigated. In a larger study with *Rhinanthus angustifolius* and 11 grass species De Hullu (1984) found that among the studied grasses were both good (e.g. *Bromus hordeaceus*, *Alopecurus geniculatus*) and very poor hosts (e.g. *Alopecurus pratensis*, *Danthonia decumbens*) for the parasite. Similarly, although grasses were on average poor hosts for *M. arvense*, not surprisingly, *Triticum aestivum* (wheat) was a good host for the former weed of cereal fields *M. arvense*.

Species from high nutrient habitats, independent of their initial size and functional group, were better hosts for *M. arvense* than species typical for nutrient-poor habitats. A tendency for species from nutrient-rich habitats to be good hosts has also been observed by De Hullu (1984) in her study of *Rhinanthus angustifolius*. Host species are known to differ in the quantity and quality of compounds they provide for hemiparasites (Govier et al., 1967; Guo and Luo, 2010; Seel and Press, 1993). Species adapted to nutrient-rich soils often have higher nutrient absorption rates from the soil (Chapin, 1980) and may have provided the parasite with more nutrients. However, differences in N-content of the hosts did not explain the effects of host habitat of origin on host quality for *M. arvense*, suggesting that other traits were more important.

Some of the species studied as hosts for *M. arvense* have been used in previous experiments with hemiparasites. While most legumes were suitable hosts for *M. arvense*, *Anthyllis vulneraria* was a very poor host despite its high N-content. However, *A. vulneraria* was a good host for *Euphrasia* spp. (Yeo, 1964). *Festuca ovina* and *Cynosurus cristatus* which were very poor hosts for *M. arvense* were good host for *Rhinanthus minor* (Cameron and Seel, 2007; Keith et al., 2004). *Medicago sativa*, the best host in the current study, was a good host for several other hemiparasites, but not for *Euphrasia minima. Plantago lanceolata*, a very

poor host for *M. arvense* in the present study and for *Rhinanthus minor* (Cameron et al., 2006), was one of the best hosts for *Euphrasia* spp. (Wilkins, 1963). The suitability of *Trifolium repens* as a host also varied strongly depending on parasite species. *T. repens* was a good host for *M. arvense* in the current experiment, for *Euphrasia* spp. (Wilkins, 1963; Yeo, 1964), and *Rhinanthus angustifolia* (De Hullu, 1984), but it was a poor host for *Odontites litoralis* and *O. verna* (Snogerup, 1982), and growth of *Orthocarpus purpurascens* and *Bellardia trixago* with *T. repens* was worse than without a host (Atsatt and Strong, 1970).

These inconsistencies in the quality of species as hosts for hemiparasites suggest specific interactions between parasite-host pairs. Resistance mechanisms of a host that are effective against one hemiparasite may not necessarily be effective against other species, and a species that is a good host for one hemiparasite is not necessarily also a good host for other parasite species, even from the same plant family.

The strong differences among species in their quality as hosts for hemiparasites imply that species composition of vegetation will have a strong influence on the performance and distribution of hemiparasites. Hemiparasites will grow well either in habitats dominated by a suitable host, e.g. cereal fields for the former weed *M. arvense*, or in species-rich habitats, where at least some species are suitable hosts (Joshi et al., 2000; Marvier and Smith, 1997). *M. arvense* today occurs in central and western Europe mainly in wayside vegetation and calcareous grasslands. Some of the dominant species in wayside habitats of *M. arvense* (Matthies 1991) like *Arrhenatherum* elatius and *Poa annua* are good hosts for the parasite. In contrast, in nutrient-poor calcareous grasslands with *M. arvense* the typical matrix species like *Bromus erectus, Koeleria pyramidata* and *Festuca ovina* (Matthies 1986; 1991) are all poor hosts. This probably restricts *M. arvense* to patches where suitable host plants grow. This view is supported by the results of a study on the species associated with *M. arvense* in a species-rich calcareous grassland. In the immediate vicinity (within a radius of 12 cm) of plants of *M. arvense* the very good host *Medicago falcata* (= *Medicago sativa* ssp. *falcata* (L.) Arcang.) was far more frequent than in plots without the parasite only 50 cm away and the number of species was higher (Matthies 1990).

4.2. Effects of nutrient levels on the parasite

Higher levels of nutrients increased the biomass of the parasite *M. arvense* with most host species and are thus likely to be one factor for the stronger growth of *M. arvense* in the more nutrient-rich wayside habitats. Both host species and nutrient levels are therefore likely to contribute to the differences in performance between parasites in nutrient-poor grasslands and

more nutrient-rich wayside habitats. The positive effect of higher nutrient levels on the growth of the hemiparasite is in agreement with the results of previous studies on hemiparasites (Matthies and Egli, 1999; Mudrák and Lepš, 2010; Tesitel et al., 2014), but as in the present study there were also exceptions to the positive effect of nutrients on parasite growth. Higher nutrient levels may increase shading of the hemiparasites by the hosts, but also influence physical characteristics of host roots that influence the probability of haustoria formation like root thickness and the number of root hairs (Davies and Graves, 2000). Increasing nitrogen supply has been found to reduce the attachment success of *Striga* (Cechin and Press, 1993a; b) and high phosphorus levels suppressed attachment of *Rhinanthus minor* to its host *Lolium perenne* (Davies and Graves, 2000). Very high nutrients levels have been suggested as an explanation why *Trifolium repens* was a comparatively poor host for *M. arvense* in a previous study (Schädler et al., 2005).

It has been suggested that nutrient addition will increase the sink strength of fast-growing host species that are highly responsive to increased nutrient supply and thus reduce their quality as hosts, while more nutrients would have little effect on the sink strength of slow-growing species (Davies and Graves, 2000). This hypothesis was not supported in the present study. The effect of more nutrients on the growth of *M. arvense* (relative difference in biomass) was neither related to the relative growth rate of host species ($r = -0.11$, $p = 0.58$), nor to their responsiveness to increased nutrient supply ($r = -0.03$, $p = 0.90$), expressed as the proportional change in mean biomass of a host species in response to the higher nutrient level. While higher nutrient levels increased the biomass of *M. arvense*, the mean effect of more nutrients on the biomass of the parasite (+33%) was much smaller than the effect on the biomass of its hosts (+98%). The much stronger increase in the growth of the hosts than of the parasite *M. arvense* in response to higher nutrient levels suggests that under field conditions of higher host densities than in the present experiment, the competitive ability of *M. arvense* will be strongly reduced at higher nutrient levels and the parasite will suffer from increased shading by the hosts, resulting in reduced survival. Similar effects of high nutrient availability have been observed in other studies (Fürst, 1931, Mudrák and Lepš, 2010; Tešitel et al., 2015).

4.3. Effects of host identity and nutrient level on biomass allocation, morphology and architecture of the parasite

When the hemiparasite *M. avense* was grown with poor hosts, the proportion of its biomass allocated to roots (root mass fraction, RMF) was similar to that of its autotrophic hosts in the experiment and to the average value given for herbaceaous plants (0.30) in a large review by

Poorter and Nagel (2000). However, grown with suitable hosts, the RMF of the parasite was very low. Parasites with more than 150 mg of biomass allocated less than 10% of their biomass to roots and thus less than all studied host species. The RMF of 0.03 of *M. arvense* plants grown with the best host *Medicago sativa* was lower than that of any of the several hundred plants in the large compilation of allocation data by Niklas and Enquist (2004). Similarly low RMF-values have been found in other studies of hemiparasites (Table 6), suggesting that root hemiparasites need less roots than autotrophic plants, because they can obtain most of the water and nutrients they require from their hosts, and thus represent a separate functional group in the sense of Poorter et al. (2012) with regard to root allocation. This notion is supported by the observation that facultative parasites grown without a host invest usually far more into their root system than when grown with a host (s. Table 6). The results of the studies compiled in Table 6 also suggest that the RMF of hemiparasites depends on their life history. Perennial herbaceous hemiparasites, whose root systems are the only plant parts that survive the winter, and hemiparasitic shrubs and trees invest considerably more into their root systems than do annual hemiparasites (Table 6).

A large part of the variation in the RMF of *M. arvense* caused by the different host plants was due to their effect on parasite size, as biomass allocation to roots decreased with the size of the parasite. A decrease in RMF with size has been found in many plant species (Wilson, 1988; Poorter et al., 2012) and such a trend can also be calculated for the hemiparasite *Thesium chinense* from the data in Guo and Luo (2010). However, even *M. arvense* plants of the same shoot mass varied considerably in their root mass, depending on the host species. This could have been due to variation in the amount of own roots the parasite needed to obtain a certain amount of water and nutrients from the host plants. In agreement with the functional equilibrium theory of biomass allocation in plants (Chapin, 1980; Iwasa and Roughgarden, 1984), a higher availability of nutrients reduced the RMF of *M. arvense*, although only slightly.

All morphological and physiological traits of the parasite *M. arvense* varied strongly with host species identity and nearly all were influenced by nutrient level. Traits like the total number of nodes, leaf width, or the number and length of branches, have been used as criteria for differentiating between subspecies and seasonal ecotypes of *Melampyrum arvense* (Hartl, 1974; Tutin et al., 1972;) and of other hemiparasitic Orobanchaceae (Jäger and Werner, 2005; Tutin et al., 1972; Zopfi, 1993). However, the strong influence of host species identity and nutrient level on these traits suggests that the discrimination of subspecies, ecotypes etc. based on these traits may be problematic. In contrast to studies on *Rhinanthus* ssp. (Jonstrup et al.,

2016; Pleines et al., 2013), in *M. arvense* the number of nodes below the first flower was also influenced by host identity.

The effects of different host species on the seed mass of *M. arvense* are likely to influence the fitness of the next generation. *M. arvense* has the largest seeds of all Orobanchaceae (c. 15 mg, Matthies, 1991; cf. also Tešitel et al., 2010), which together with the parasitic habit may be responsible for the ability of the annual plant *M. arvense* to persist in closed grassland communities (Matthies, 1986; 1991). Large seeds of *M. arvense* produce large seedlings (Matthies, 1991), whose roots may have a better chance to encounter the roots of a suitable host and attach to them, and are likely to be more able to grow through accumulated litter. Both the survival and final size of plants of *M. arvense* in the field have been shown to strongly increase with the size of seedlings (Matthies 1991).

The effects of higher nutrient availability on most morphological traits of the parasite *M. arvense* can be understood as simple consequences of an overall increase in the size of the parasite, because adjusted for differences in size, nutrient level had no effect on these traits. In contrast, the strong effects of host identity on all traits of *M. arvense* could only be partly explained by changes in plant size. Parasites of the same overall size (biomass) that had grown with different hosts differed strongly in traits like height, leaf length and number, inflorescence length and individual seed mass. This shows that the host species influenced not only the overall size of the parasites, but also their morphology and architecture. Few previous studies have investigated possible host effects on the morphology and allocation patterns of hemiparasites. Snogerup (1982) noticed that when *Odontites verna* was grown with *Plantago maritima* as host, its leaves became succulent and its branching pattern changed. Seel and Press (1993) found effects of host type on the allocation of above-ground biomass to various plant parts by *Euphrasia frigida* and *Rhinanthus minor* growing on legumes and grasses in the arctic. In an experiment with the parasites *Euphrasia minima* and *Odontites vulgaris* the identity of the host species (*Medicago sativa* or *Lolium perenne)* influenced the allocation of above-ground biomass to stems, leaves and reproductive parts of the parasites (Matthies, 1998). However, in these studies it can not be excluded that the differences in allocation patterns observed were a byproduct of differences in parasite size, as effects were not adjusted for differences in biomass. A clear effect of host species on reproduction was found in an experiment with *Castilleja wightii*, which produced 78% more flowers when grown with *Eriophyllum staechadifolium* as host than with *Lupinus arboreus*, although its biomass was lower (Marvier 1996). The composition and relative amount of compounds taken up by parasites from their hosts have been found to differ strongly depending on the host species

(Govier et al., 1967; Pate, 2001; Tennakoon and Pate, 1996) and this may influence the growth patterns of the parasites and the quality of their tissue.

4.4. Effects of the parasite M. arvense *on the biomass of host species*

Strong negative effects of root hemiparasites on the growth and reproduction of their host plants have been found in both pot (e.g. Li et al., 2012a; Malcolm, 1964; Marvier, 1996; Matthies, 1995a; b; 1996; 1997; 1998; Matthies and Egli, 1999) and field studies (Davies et al., 1997; Fürst, 1931; Joshi et al., 2000; Marvier, 1998b; Mizianty, 1975; references in Ameloot et al., 2005; Press and Phoenix, 2005). A review of the effect of *Rhinanthus* ssp. concluded that the above-ground biomass of co-occurring species was reduced by on average 40% in field studies and 60% in pot experiments (Ameloot et al., 2005). *M. arvense* was formerly a noxious weed of cereals that can at a density of 24 per m^2 reduce the number of wheat spikeletts by 29% and the number of grains per ear by 79% (Benkov, 1978). In a pot experiment, *M. arvense* reduced the total biomass of *Medicago sativa* by 53% (Matthies, 1995a), and in another experiment the parasite reduced the shoot mass of *Lolium perenne* by 19%, that of *Linum usitatissiumum* by 56% and that of *M. sativa* by 64% (Matthies, 1996). The reduced growth of plants in the presence of parasites is to a large degree due to the loss of water and solutes caused by parasitism (Jiang et al., 2003, Phoenix and Press, 2005), which may in turn also result in reduced photosynthesis of the host (Cameron et al., 2008; Watling and Press, 2001). In contrast, the competitive effect due to the direct uptake of water and nutrients from the soil by the roots of hemiparasites is likely to be small because of the small root system of hemiparasites attached to a host. Similarly, competition for light by the shoots of hemiparasites has been shown to have little effect on host growth (Matthies, 1995a; b).

In the present study, the hemiparasite *M. arvense* reduced the biomass of nearly all the plant species with which it was grown, but the effect varied strongly among species. The damage to the host increased with the biomass of the parasite, i.e. good hosts were far more suppressed than poor hosts, suggesting that the degree of host damage can be explained to a large extent in terms of source - sink relationships. Similar conclusions have been drawn from other studies (Atsatt and Strong, 1970; Gibson and Watkinson, 1991; Li et al., 2012a; Matthies, 1995a; 1996; 1997). However, in these studies only a few species were compared and no formal analysis of the relationship between benefit to a parasite and damage to the host was possible. While the damage to a host species increased clearly with the size of the parasite *M. arvense*, there was still huge variation in the degree of damage to relatively good hosts that supported parasites of similar size, indicating that different host species varied in their

tolerance of parasitism. Species like *Lotus corniculatus*, *Trifolium pratense* and *Arrhenatherum elatius* were good hosts for *M. arvense*, but nevertheless hardly damaged, whereas the biomass of *Capsella bursa-pastoris* was strongly reduced.

A multiple regression analysis of traits that may influence a species' sensitivity to parasitism by *M. arvense* indicated that grasses were far less affected than legumes and forbs, which can be attributed to their mostly poor quality as hosts, and that sensitivity to parasitism depended on the relative growth rate of host species. The mostly weak effect of *M. arvense* on the growth of grasses is in strong contrast to the result of studies on the effect of *Rhinanthus* ssp. which usually suppress grasses much more than non-leguminous forbs (Bardgett et al., 2006; Cameron et al., 2006; Davies et al., 1997; Hellström et al., 2011; Joshi et al., 2000; Mizianty, 1975; Mudrák and Lepš, 2010; Westbury and Dunnett, 2007; 2008). Increases in the biomass of grasses, but not of forbs, after removal of the hemiparasites *Pedicularis canadensis* from a restored prairie in the USA (Borowicz and Armstrong, 2012) and of *Parentucellia viscosa* from a floodplain in Japan (Suetsugu et al., 2012) also indicated particularly strong effects of hemiparasites on grasses. The stronger negative effects of parasitism by *Rhinanthus* on grasses than forbs have been attributed to lower resistance of the roots of grasses against the parasite (Cameron et al., 2006; Rümer et al., 2007). However, the weaker effects of *M. arvense* on grasses than on forbs indicate that both the lack of resistance observed in some grasses against *Rhinanthus* and the strong resistance in some forbs cannot be generalised.

The smaller reduction in the biomass of host species with a high relative growth rate (RGR) in the present study suggests that within each functional group fast-growing plants were better able to compensate for the loss of water and solutes to the parasite than slow-growing plants. Similar benefits of a high RGR have been observed for plant tolerance to herbivory (Strauss and Agrawal, 1999). In contrast, Li et al. (2012b) based on an experiment with the shoot parasite *Cuscuta chinensis* and six host species concluded that damage to a host was positively related to its RGR.

Because the growth of individual species is reduced to very different degrees by *M. arvense,* the hemiparasite may change the competitive balance between species (Matthies, 1996). Similar observations have been made for other species (Joshi et al., 2000; Pennings and Callaway, 1996; 1998; Marvier, 1998a; Niemelä et al., 2008; Phoenix and Press, 2005a). The great differences in susceptibility observed for species that commonly co-occur with *M. arvense* suggest that the effects on the competitive balance between species may be very strong in the habitats of the parasite. The effects of parasites on community diversity will

depend on whether the preferred hosts are dominants or subdominants in a habitat (Phoenix and Press, 2005a). In the case of *M. arvense*, matrix species from calcareous grasslands like *Bromus erectus* and *Festuca ovina* were hardly affected by the parasite. *Arrhenatherum elatius*, one of the dominant species of the more nutrient-rich habitats of *M. arvense*, was also little affected by the parasite although it was a good host. The results suggest that *M. arvense* might affect some of the rarer members of its communities, if it happens to grow next to them, in particular legumes like *Medicago lupulina* and *M. sativa* spp. *falcata*.

In the current study, the parasite *M. arvense* was grown with two individuals of the same host species at opposite sides of the parasite. Interestingly, however, the parasite usually damaged one of the host individuals more than the other one, leading to an increase in size inequality of the host individuals compared to the no-parasite control. Genetic differences in susceptibility could be responsible for this, but it is more likely that roots of one the host individuals were by chance attacked first, which may have locally stimulated parasite root growth and haustoria formation. Similar effects of hemiparasites on their hosts under field conditions are to be expected and will result in an increase in the size variability of the host population.

Because the negative effect of root hemiparasites on their hosts is to a large extent due to the loss of nutrients to the parasites, it may be expected that the impact of a parasite on its host is greatest at low nutrient levels, i.e. when the resources taken up by the parasites are limiting (Matthies and Egli, 1999; Phoenix and Press, 2005a; Westwood, 2013). Such a higher impact of parasites on their hosts at low nutrient levels has been found in some studies (Cameron et al., 2005; Cechin, 1993b; 1994; Davies and Graves, 2000; Gibson and Watkinson, 1991; Jiang et al., 2010; Matthies and Egli, 1999). In contrast, in the present study the strength of host suppression by the parasite *M. arvense* was not influenced by nutrient level, in line with the results of several other studies in mesocosms (Bardgett et al., 2006) and in the field (Borowicz and Armstrong, 2012; Mudrák and Lepš, 2010).

4.5. Parasite effects on biomass allocation of the hosts

Root hemiparasites may not only reduce the overall growth of their hosts, but also influence host allocation patterns, in particular the proportion of biomass allocated to roots (root mass fraction, RMF). The parasite *M. arvense* increased the RMF of most hosts, but the effect varied depending on host species and increased with the suitability of a species as a host for *M. arvense* and the degree to which the growth of the host was suppressed. Root parasitism particularly reduces the availability of resources taken up by the roots like water and nutrients

to the host plants. A higher allocation of biomass to roots by host plants in reaction to root parasitism is thus in accordance with the functional equilibrium hypothesis of plant growth that predicts increased allocation by plants to organs that can alleviate the scarcity of a limiting resource (Chapin, 1980). Correspondingly, studies of the effects of the stem parasite *Cuscuta* have found increases in biomass allocation to host shoots (Jeschke et al., 1994; Jeschke and Hilpert, 1997; Shen et al., 2005). However, an increased allocation of biomass to roots and correspondingly less to above-ground parts in response to root parasitism could also be seen as a successful manipulation of the host by the parasite, as it leads to a relative increase in the parts of the hosts useful to the parasite and reduces competition for light by the above-ground parts of the host.

The results of previous studies on the effects of root hemiparasites on host RMF have been variable. Studies of the effects of *Striga* ssp. have found with very few exceptions (e.g. a tolerant host variety) strong increases in the RMF of the host species in response to parasitism (Table 7). In some studies, host plants increased in response to parasitism by *Striga* not only their relative allocation of biomass to roots, but actually increased absolute root growth (Parker, 1984; Taylor et al., 1996). A similar effect has been observed in response to the related parasite *Alectra vogelii* (Rambakudzibga et al., 2002). Both *Striga* and *Alectra* are parasites that can have very strong negative effects on their hosts, reduce host growth even before emergence from the soil, have low rates of photosynthesis and resemble in many respects holoparasites (de la Harpe et al., 1979; Parker and Riches, 1993; Press et al., 1987; Rambakudzibga et al., 2002).

The results of studies on the effect of root hemiparasites other than *Striga* and *Alectra* on host RMF have been less consistent (Table 7). While several studies found increases in host RMF in response to parasitism, others found no significant effects or even reductions in host RMF. It is notable that all the host plants that in previous studies were found to reduce their allocation to roots, as well as several of those that showed no significant response, were legumes, mostly *Medicago sativa*. A possible explanation could be that loss of nitrogen to the parasite is important for the reaction of the hosts. In contrast to other plants, legumes might react to a loss of nitrogen to a root parasite by increasing the carbohydrate supply to their nitrogen-fixing symbionts, which would require higher allocation of biomass to above-ground parts. However, the response of legumes is not consistent and in the current study legumes increased their RMF most strongly in response to parasitism by *M. arvense*, while most grasses did not respond or even slightly reduced their RMF. The weak response of grasses to the parasite in terms of biomass allocation can be related to their mostly poor quality as hosts

for *M. arvense*, as species that were good hosts and whose growth was strongly reduced by the parasite increased their allocation to roots more strongly. A potential weakness of most previous studies (but see Cechin and Press, 1993b; Rambakudzibga et al., 2002) is that they did not test whether parasite-induced changes in host RMF might be explained simply by a reduction in overall host size. However, both in the current and in the other studies that investigated possible effects on host allometry, parasitism did cause changes in host allometry. The functional equilibrium theory of plant growth would predict a smaller effect of root parasitism on host RMF at high nutrient levels (Poorter et al., 2012). This has been observed in *Striga* - host plant associations (Cechin and Press, 1993b; 1994), but not in the present study.

4.6. Parasite effects on total productivity

The combined biomass of hemiparasites and their hosts is usually lower than that of the hosts grown without the parasites (Matthies, 1995 a; b; 1997; 1998, Matthies and Egli, 1999; for the effects of *Rhinanthus* see review by Ameloot et al., 2005; Ameloot et al., 2008; Bardgett et al., 2006; Hautier et al., 2010; Hellström et al, 2011; Mudrák and Lepš, 2010; Tešitel et al., 2015). This reduction in productivity has been attributed to the lower resource efficiency of the parasites (Matthies, 1995a), as hemiparasites have much higher transpiration rates (Phoenix and Press, 2005a; Press et al., 1988; 1993) and higher tissue nutrient concentrations (Pate et al., 1990; Phoenix and Press, 2005a; Seel et al., 1993; this study), but similar or lower rates of photosynthesis (Press et al., 1988; 1993) than their hosts. A reduction of overall productivity by hemiparasites has, however, not been observed in all experiments. Hwangbo et al. (2003) found no effect of *Rhinanthus minor* on total productivity in a pot experiment with *Poa pratensis* as host. In several recent field studies of *Rhinanthus* no effect of the parasite on total biomass was observed (Hellström et al., 2011; Westbury and Dunnett, 2008) or very small effects (Westbury and Dunnett, 2007), in spite of reductions in host biomass. In a field study with *R. alectorolophus*, the presence of the parasite had no effect on total biomass in high diversity plots, but actually increased total biomass in low diversity plots (Joshi et al., 2000).

In the present study, the effect of *M. arvense* on total productivity depended on the host species and nutrients. Under most conditions the parasite reduced total biomass, but there were some exceptions. Most remarkable was the behaviour of the combination of *M. arvense* and *Capsella bursa-pastoris.* At high nutrient levels *M. arvense* reduced the growth of its host *Capsella* by more than 50%, but this reduction in host biomass was more than compensated

by the very strong growth of the parasite that produced more than twice the biomass of its host, leading to an overall increase in productivity of more than 60%. A possible explanation relates to the observation that *C. bursa pastoris,* which is an annual species with determinate growth, had finished growing and switched to reproduction relatively early in the experiment, while the parasite *M. arvense* continued to grow. The root system of *C. bursa patoris* was apparently capable of supporting far more transpiring tissue that than just its own shoot. This behaviour of the *M. arvense* - *C. bursa pastoris* system, like the observations of Joshi et al. (2001), is in contrast to the prediction by the model of Hautier et al. (2010) that the combined mass of the host-parasite system is always less than the mass of the host grown alone.

5. **Conclusions**

By studying the growth of the hemiparasite *M. arvense* with many different host species, this study showed that individual species may differ enormously in their quality as hosts for hemiparasites and that many common species are unsuitable as hosts. This supports the view that a species-rich vegetation can be important for conserving threatened hemiparasites like *M. arvense* (Marvier and Smith 1997).

Part of the variation in the quality of species as hosts was due to their functional group, with legumes the best hosts, followed by non-leguminous forbs, while most grasses were rather poor hosts. This pattern of host quality is in strong contrast to that observed in the best studied hemiparasite *Rhinanthus minor*, whose growth is much better with grasses than forbs as hosts, and suggests that hemiparasite - host species interactions may be parasite-specific. Moreover, the current study with many replicates for the three functional groups clearly showed that host quality may vary strongly within functional groups and is difficult to predict.

Host species identity influenced in contrast to nutrient levels not only the growth of hemiparasites, but also their architecture and morphology. The strong influence of host identity on morphological traits of *M. arvense*, among them traits that have been used to define infraspecific taxonomic units, suggests that caution is necessary when interpreting morphological variation among hemiparasite populations observed in the field. The result that biomass allocation to roots (RMF) decreases strongly with host quality, indicates, together with the results of the extensive literature review of RMF in root hemiparasites, that reduced investment into roots may be one of the principal benefits of the hemiparasitic lifestyle, although only for annual plants. In perennial hemiparasites such a strong reduction of the root system is apparently not possible because of the importance of a large root system to ensure survival of the adverse season. The advantages of a reduction of the root system in annual

hemiparasites may help to explain why annual parasites have evolved several times in the hemiparasitic Orobanchaceae (s. Těšitel et al., 2010).

The impact of the hemiparasite *M. arvense* on the growth of suitable hosts was very strong and may change the competitive balance between species in nature (Matthies 1996). The loss of an endangered parasitic plant like *M. arvense* has therefore the potential to reduce habitat heterogeneity and change the distribution and abundance of other species in its habitat (see Grewell 2008). The differences in damage to the growth of species that are of similar quality as hosts for *M. arvense* indicate that not only resistance but also tolerance of parasitism may be important in determining how strongly species are negatively affected by the presence of a root hemiparasite. There are clear paralleles to the different reponses of plants to herbivory (Strauss and Agrawal 1999).

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Figure legends

Fig. 1. The effect of different host species and two nutrient levels on (a) shoot mass and (b) root mass of the hemiparasite *Melampyrum arvense*. From top to bottom the host species are in order of decreasing total biomass (shoot + root mass; means over both nutrient levels). Means +1 SE.

Fig. 2. The relationship between proportion of biomass allocated to roots (root mass fraction) by the parasite *M. arvense* grown with different host species and its total biomass. For abbreviations of host species names see Table 1.

Fig. 3. Probability of flowering as a function of total biomass in the hemiparasite *M. arvense*.

Fig. 4. The ratio between the nitrogen content of the shoots of the hemiparasite *M. arvense* and that of the shoots of their hosts. Values greater one indicate a higher nitrogen concentration in parasite than in host tissue. From top to bottom the host species are in decreasing order of host quality (see Fig. 1a). Means +1 SE. Asterisks indicate significant differences between the nitrogen content of parasite and host shoots. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

Fig. 5. The relationship between (a) nitrogen content and (b) leaf chlorophyll content and biomass for individuals of the hemiparasite *M. arvense*. Note log-scales for chlorophyll content and biomass.

Fig. 6. (a) Root mass of individuals of the hemiparasite *M. arvense* of 1 g of shoot mass grown with different host plants. (b) - (h) Mean trait values of individuals of *M. arvense* of 1 g total biomass grown with different host plants: (b) parasite height, (c) number of leaves, (d) cumulative branch length, (e) inflorescence length, (f) mass per seed, (g) leaf chlorophyll content, and (h) parasite nitrogen content. (a), (c), (d), (g), and (h) show values for parasites grown at high nutrient levels, because these traits were also influenced by nutrient levels, the other figures show means over both nutrient levels, as nutrient level had no significant effect on the traits depicted (see Table 4). Shown are only the effects of the 15 hosts with which at least one of the individuals of the parasite *M. arvense* produced a biomass of more than 1 g. Predicted means +1 SE. For abbreviations of host species names see Table 1.

Fig. 7. Partial regression plot showing the effect of mean host size at the start of the experiment on mean final parasite biomass, adjusted for the effects of host functional group and nutrient status of host habitat.

Fig. 8. The effect of (a) host functional group and (b) nutrient status of host habitat on final parasite biomass. Effects are adjusted for those of initial host size and (a) nutrient status and (b) host functional group. Means +1 SE.

Fig. 9. Reduction in the mean shoot mass of different host species due to the hemiparasite *M. arvense* in relation to the mean biomass the parasite produced with each host species. For abbreviations of host species names see Table 1.

Fig. 10. The effect of the hemiparasite *M. arvense* on the root mass fraction (RMF) of different host species. A point on the bisecting line indicates that the RMF of that species was not influenced by the parasite, points above the bisecting line indicate that the parasite caused an increase in the investment into roots, points below the line indicate a decrease. For abbreviations of host species names see Table 1.

Fig. 11. The effect of the hemiparasite *M. arvense* on overall productivity, i.e. the combined biomass of hosts and parasite, when grown with different host species at two nutrient levels. From top to bottom the host species are in decreasing order of host quality for the parasite (mean total biomass).

Table 1
Species used as host plants for the hemiparasite *M. arvense* in the experiment. The indicator value for nutrients (N-value, Ellenberg et al. 1992) indicates the realised ecological niche of a species with respect to nutrient level in Central Europe. Species with N-values of 2-3 were classified as species of low-nutrient habitats, those with N-values of 4-6 as species of medium-nutrient habitats, and those with N-values of 7-8 as species of high-nutrient habitats. Species for which no N-values were available were classified as indicating moderately nutrient-rich habitats, except for the crop plant *Triticum aestivum*.

Host species	Species code	Family	N-value	Nutrient status of habitat	Functional group
Hieracium pilosella L.	Hp	Asteraceae	2	Low	Forb
Sanguisorba minor Scop.	Sm	Rosaceae	2	Low	Forb
Chrysanthemum leucanthemum L.	Cl	Asteraceae	3	Low	Forb
Festuca ovina L.	Fo	Poaceae	2	Low	Grass
Koeleria pyramidata (Lam.) P. Beauv.	Kp	Poaceae	2	Low	Grass
Bromus erectus Hudson	Be	Poaceae	3	Low	Grass
Anthyllis vulneraria L.	Av	Fabaceae	3	Low	Legume
Lotus corniculatus L.	Lc	Fabaceae	3	Low	Legume
Achillea millefolium L.	Am	Asteraceae	4	Medium	Forb
Capsella bursa-pastoris (L.) Med.	Cb	Brassicaceae	5	Medium	Forb
Matricaria chamomilla L.	Mc	Asteraceae	5	Medium	Forb
Myosotis arvensis L. (Hill)	Ma	Boraginaceae	6	Medium	Forb
Papaver rhoeas L.	Pr	Papaveraceae	6	Medium	Forb
Plantago lanceolata L.	Pl	Plantaginaceae	.	Medium	Forb
Daucus carota L.	Dc	Apiaceae	4	Medium	Forb
Trisetum flavescens (L.) P. Beauv.	Tf	Poaceae	5	Medium	Grass
Cynosurus cristatus L.	Cc	Poaceae	4	Medium	Grass
Dactylis glomerata L.	Dg	Poaceae	6	Medium	Grass
Medicago lupulina L.	Ml	Fabaceae	.	Medium	Legume
Medicago sativa L.	Ms	Fabaceae	5	Medium	Legume
Trifolium pratense L.	Tp	Fabaceae	.	Medium	Legume
Taraxacum officinale (L.) Web.	To	Asteraceae	7	High	Forb
Urtica dioica L.	Ud	Urticaceae	8	High	Forb
Arrhenatherum elatius L.	Ae	Poaceae	7	High	Grass
Triticum aestivum L.	Ta	Poaceae	.	High	Grass
Poa annua L.	Pa	Poaceae	8	High	Grass
Trifolium repens L.	Tr	Fabaceae	7	High	Legume

Table 2
The effect of host species and nutrient level on traits of the hemiparasite *Melampyrum arvense*. Results of analyses of variance. Significant effects ($p < 0.05$) are in bold face.

Trait	Host		Nutrients		Nutrients x Host		df_{host}	df_{res}
	F	P	F	P	F	P		
Shoot mass (log)	38.00	**<0.001**	11.67	**<0.001**	1.62	**0.030**	26	331
Root mass (log)	28.70	**<0.001**	6.34	**0.012**	2.16	**0.001**	26	331
Root mass fraction (log)	13.58	**<0.001**	5.33	**0.022**	0.91	0.600	26	331
Height	37.25	**<0.001**	4.97	**0.031**	1.98	**0.004**	26	331
Leaf length	29.86	**<0.001**	2.17	0.142	1.50	0.059	26	331
Leaf width	27.13	**<0.001**	2.71	0.101	1.53	0.050	26	331
Leaf number (log)	31.31	**<0.001**	9.43	**0.002**	1.39	0.101	26	331
Branch length (log)	37.30	**<0.001**	11.56	**<0.001**	2.07	**0.002**	26	331
Length of internodes	12.86	**<0.001**	2.27	0.133	1.18	0.265	25	240
Number of vegetative nodes	2.30	**<0.001**	0.30	0.582	1.08	0.373	25	240
Seed mass	2.30	**0.003**	6.56	**0.012**	0.86	0.638	19	110
Stem diameter (log)	28.43	**<0.001**	6.08	**0.014**	1.68	**0.022**	26	331
Inflorescence length (log)	35.30	**<0.001**	11.53	**<0.001**	2.19	**<0.001**	26	331
Leaf chlorophyll content (log)	25.95	**<0.001**	18.63	**<0.001**	1.02	0.436	26	331
Nitrogen content	52.0	**<0.001**	3.83	0.051	1.97	**0.004**	26	331

Table 3
The influence of different host species on various morphological and physiological traits of the hemiparasite *Melampyrum arvense.* Seed mass is missing if none of the parasites did fruit with a host. Host species are in order of descending parasite mass.

Host species	Height (cm)	Branch length (cm)[a]	Number of leaves[a]	Length of inflores-cence (cm)[a]	Stem diameter (mm)[a]	Leaf length (mm)	Leaf width (mm)	Number vegetative nodes	Mean seed mass (mg)	Chloropyll content (μg cm^{-2})[a]	Nitrogen content (%)
Medicago sativa	35.2	185.5	160.0	53.9	2.9	58.2	8.1	9.9	14.6	46.7	3.6
Achillea millefolium	32.6	86.3	88.5	19.5	2.1	56.7	7.8	10.7	13.7	22.2	1.1
Sanguisorba minor	29.6	65.4	64.2	14.8	1.9	53.9	7.0	10.1	15.1	26.3	1.2
Matricaria chamomilla	32.9	56.2	68.5	10.8	1.7	52.3	7.2	10.6	14.3	19.4	1.0
Taraxacum officinale	30.7	51.2	68.1	9.2	1.7	51.1	7.1	10.9	17.9	19.3	1.0
Poa annua	27.1	46.9	58.6	10.3	1.7	45.6	6.0	10.5	12.9	20.6	1.2
Arrhenatherum elatius	26.7	34.0	47.1	5.8	1.3	43.5	5.5	10.8	17.0	23.2	1.3
Trifolium pratense	26.5	49.8	53.6	10.3	1.4	41.1	6.1	10.0	14.7	31.6	2.1
Urtica dioica	23.1	31.0	48.0	4.9	1.3	38.1	5.4	11.3	14.7	23.1	1.3
Medicago lupulina	22.3	28.4	49.3	4.8	1.4	36.6	5.3	10.7	20.7	27.5	2.2
Triticum aestivum	24.9	33.1	52.4	6.5	1.3	39.6	5.7	10.6	14.6	17.1	1.2
Capsella bursa-pastoris	21.8	32.8	43.9	5.5	1.3	34.5	4.8	10.9	11.8	16.2	1.2
Lotus corniculatus	22.4	35.0	53.8	7.4	1.3	38.2	5.4	11.0	20.0	28.2	2.2
Trifolium repens	24.5	39.6	46.2	8.3	1.2	45.9	5.5	10.5	12.7	29.3	2.4
Myosotis arvensis	18.0	18.3	31.4	2.4	0.9	34.7	4.1	10.9	9.1	13.0	1.0
Hieracium pilosella	14.6	13.5	28.5	1.4	0.9	31.7	3.8	11.2	11.2	14.0	1.0
Chrysanthemum leucanthemum	14.2	13.6	29.7	1.4	0.9	29.0	3.7	11.3	13.2	13.0	1.0
Festuca ovina	12.3	11.6	23.9	0.8	0.8	25.6	3.1	11.9	15.8	12.2	0.9
Plantago lanceolata	12.7	11.3	25.2	0.8	0.8	28.4	3.2	11.7	12.5	14.0	1.0
Daucus carota	10.3	9.1	22.8	0.7	0.8	25.2	3.0	11.2	15.6	11.9	1.0
Anthyllis vulneraria	9.5	9.1	21.5	0.5	0.8	22.1	2.3	11.6	-	13.0	1.2
Bromus erectus	9.9	8.8	17.4	0.5	0.7	23.8	2.8	11.0	-	9.9	0.9
Koeleria pyramidata	9.2	8.3	18.7	0.4	0.7	21.9	2.4	11.4	-	12.0	1.3
Cynosurus cristatus	8.3	7.6	19.8	0.2	0.6	19.9	2.2	10.0	-	10.6	0.8
Dactylis glomerata	9.3	8.8	19.6	0.1	0.6	21.6	2.3	11.5	-	9.6	0.9

Papaver rhoeas	7.8	7.2	16.2	0.2	0.7	17.9	2.2	10.0	-	10.6	1.8
Trisetum flavescens	6.6	6.4	17.5	0.0	0.6	17.4	1.9	-	-	9.7	0.9

[a]Backtransformed means of log-transformed data (geometric means).

Table 4
Results of general linear models relating various morphological and physiological traits of the hemiparasite *M. arvense* to log(biomass) of the parasite (log shoot mass in the case of root mass), host species and nutrient level. Residual df = 277. In the case of inflorescence length, df for host = 25 and residual df = 185; in the case of seed mass, df for host = 19 and residual df = 77. Significant effects ($P < 0.05$) in bold face.

Trait	Log biomass [or shoot mass] (df = 1)		Host (df = 26)		Nutrients (df = 1)		Nutrients x Host (df = 26)		Log biomass [shoot mass] x Host (df = 26)		Log biomass [shoot mass] x Nutrients (df = 1)		Log biomass [shoot mass] x Host x Nutrients (df = 26)	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Root mass (log)	6588.8	**<0.001**	6.5	**<0.001**	1.7	0.188	3.1	**<0.001**	6.8	**<0.001**	<0.1	0.852	1.8	**0.009**
Height	5059.6	**<0.001**	5.5	**<0.001**	2.6	0.110	1.2	0.240	2.6	**<0.001**	0.2	0.695	1.3	0.130
Leaf length	2211.1	**<0.001**	4.4	**<0.001**	2.8	0.095	1.2	0.224	0.9	0.555	0.6	0.444	1.2	0.239
Leaf width	1721.9	**<0.001**	2.0	**0.003**	1.2	0.283	1.1	0.332	1.5	**0.047**	0.1	0.758	0.6	0.958
Leaf number (log)	3463.3	**<0.001**	3.4	**<0.001**	0.3	0.590	1.5	0.072	1.6	**0.042**	0.3	0.610	1.7	**0.025**
Branch length (log)	9734.6	**<0.001**	7.5	**<0.001**	0.3	0.556	1.6	**0.043**	4.1	**<0.001**	1.4	0.234	0.9	0.478
Seed mass	9.1	**0.004**	2.2	**0.010**	2.5	0.121	1.0	0.523	0.5	0.970	0.2	0.682	1.2	0.392
Stem diameter (log)	2492.1	**<0.001**	2.2	**<0.001**	<0.1	0.811	0.8	0.757	3.2	**<0.001**	<0.1	0.864	1.1	0.320
Inflorescence length (log)	2935.9	**<0.001**	5.1	**<0.001**	2.7	0.105	1.0	0.474	1.4	0.114	2.9	0.090	1.5	0.087
Leaf chlorophyll content (log)	1057.3	**<0.001**	8.5	**<0.001**	9.2	**0.003**	1.2	0.205	2.1	**0.001**	1.1	0.292	0.9	0.624
% Nitrogen	273.9	**<0.001**	44.0	**<0.001**	4.0	**0.046**	2.1	**<0.002**	1.6	**0.033**	0.8	0.381	1.1	0.393

Table 5
The effect of host species, nutrient level and the presence of the hemiparasite *Melampyrum arvense* on host biomass, the coefficient of variation between the shoot mass of the two host individuals in a pot, root mass fraction of the host, host nitrogen content and total biomass produced per pot (host + parasite). Results of analyses of variance. In the case of shoot mass variation, the df for host species and its interactions are only 25, and the df_{res} 530, because shoots of the two individuals of *Trifolium repens* could not be separated. Significant effects ($P < 0.05$) are in bold face.

Source of variation		Host biomass (log)		Shoot mass variation		RMF		Host nitrogen		Total biomass per pot	
	df	F	P	F	P	F	P	F	P	F	P
Host species	26	101.32	**<0.001**	7.88	**<0.001**	99.88	**<0.001**	107.88	**<0.001**	114.20	**<0.001**
Nutrient level	1	385.61	**<0.001**	0.10	0.758	1.05	0.306	93.57	**<0.001**	474.78	**<0.001**
Parasite	1	72.78	**<0.001**	12.89	**<0.001**	17.01	**<0.001**	7.14	**0.008**	17.88	**<0.001**
Host x Nutrient level	26	3.54	**<0.001**	1.02	0.434	3.20	**<0.001**	1.56	**0.039**	3.78	**<0.001**
Host x Parasite	26	3.09	**<0.001**	1.33	0.130	1.65	**0.024**	1.52	0.050	0.74	0.819
Parasite x Nutrient level	1	2.30	0.130	0.41	0.522	7.97	**0.005**	3.23	0.073	2.13	0.145
H x N x P	26	1.17	0.262	0.81	0.734	1.22	0.207	0.68	0.885	1.52	0.050
Residual	547										

Table 6
The proportion of total biomass allocated to roots (root mass fraction, RMF) by various root hemiparasites grown without or with a host. ns, difference between biomass of parasite grown with and without host not significant. For the calculation of mean values for the RMF of annual, perennial and woody root hemiparasites only one value for each species was used (the mean over all studies).

Hemiparasite species	Life form	RMF no host	RMF with host	Host species	Source
Castilleja miniata	perennial	0.28	> 0.17	*Medicago sativa*	Matthies (1997)
Rhinanthus serotinus	annual	0.28	> 0.05	*Medicago sativa*	Matthies (1995a)
Rhinanthus serotinus	annual	0.24	> 0.10[3]	*Hordeum vulgare*	Klaren and Janssen (1978)
Rhinanthus minor	annual	0.17	> 0.04	*Hordeum vulgare*	Jiang et al. (2007)
Rhinanthus minor	annual	0.26 - 0.39[2]			Seel et al. (1993b)
Rhinanthus serotinus	annual		0.05/ 0.07[5]	*Agrostis capillaris*	Salonen and Puustinen (1996)
Odontites verna	annual	0.07	> 0.06	*Trifolium repens*	Govier (1966)
Odontites verna	annual	0.07	> 0.05	*Hordeum vulgare*	Govier (1966)
Odontites rubra	annual	0.22	> 0.08	*Medicago sativa*	Matthies (1995a)
Odontites vulgaris (*rubra*)	annual	0.14	> 0.07	*Medicago sativa*	Matthies (1998)
Castilleja chromosa	perennial	0.16	> 0.08	*Medicago sativa*	Matthies (1997)
Euphrasia minima	annual	0.07	> 0.04	*Lolium perenne*	Matthies (1998)
Orthocarpus purpurascens	annual	0.06	> 0.03	*Lolium perenne*	Matthies (1997)
Melampyrum arvense	annual	[0.12][1]	> 0.03	*Medicago sativa*	Matthies (1995b)
Melampyrum arvense	annual		0.03 - 0.24	27 species	This study
Pedicularis rex	perennial	0.33	> 0.13	*Hordeum vulgare*	Li et al. (2012a)
Pedicularis rex	perennial	0.33	> 0.13	*Trifolium subterraneum*	Li et al. (2012a)
Thesium chinense	perennial	0.23	> 0.13	*Chrysanthemum indicum*	Guo and Luo (2010)
Thesium chinense	perennial	0.23	> 0.15	*Artemisia japonica*	Guo and Luo (2010)
Thesium chinense	perennial	0.23	> 0.20 (ns)	*Triticum aestivum*	Guo and Luo (2010)
Thesium chinense	perennial	0.23	> 0.13	*Imperata cylindrica*	Guo and Luo (2010)
Thesium chinense	perennial	0.23	> 0.12	*Prunella vulgaris*	Guo and Luo (2010)
Thesium chinense	perennial	0.23	> 0.17	*Eremochloa ophiuroides*	Guo and Luo (2010)
Thesium chinense	perennial	0.23	> 0.14	*Cynodon dactylon*	Guo and Luo (2010)
Thesium humile	annual	0.10	> 0.04	*Triticum vulgare*	Fer et al. (1994)
Santalum album	tree	0.58	> 0.46	*Eucalyptus camaldulensis*	Radomiljac et al. (1999)
Santalum album	tree	0.58	> 0.42	*Acacia trachycarpa*	Radomiljac et al. (1999)
Santalum album	tree	0.58	> 0.35	*Sesbania formosa*	Radomiljac et al. (1999)

Santalum album	tree	0.58	> 0.31	*Acacia ampliceps*	Radomiljac et al. (1999)
Santalum spicatum	tree	0.58 - 0.74			Wijesuriya and Fox (1985)
Orthocarpus purpurascens	annual	0.06	≅ 0.06	*Medicago sativa*	Matthies (1997)
Odontites vulgaris	annual	0.14	≅ 0.14 (ns)	*Lolium perenne*	Matthies (1998)
Euphrasia minima	annual	0.07	≅ 0.07 (ns)	*Medicago sativa*	Matthies (1998)
Thesium chinense	perennial	0.23	≅ 0.20 (ns)	*Gnaphalium affine*	Guo and Luo (2010)
Pedicularis rex	perennial	0.33	≅ 0.26 (ns)	*Medicago truncatula*	Li et al. (2012a)
Pedicularis tricolor	perennial	0.21	≅ 0.21 (ns)	*Hordeum vulgare*	Li et al. (2012a)
Pedicularis tricolor	perennial	0.21	≅ 0.21 (ns)	*Medicago truncatula*	Li et al. (2012a)
Pedicularis tricolor	perennial	0.21	≅ 0.28 (ns)	*Trifolium subterraneum*	Li et al. (2012a)
Pedicularis cephalantha	perennial	0.21	≅ 0.35 (ns)	*Trifolium repens*	Ren et al. (2010)
Pedicularis cephalantha	perennial	0.21	≅ 0.32 (ns)	*Polypogon monspeliensis*	Ren et al. (2010)
Pedicularis kansuensis	annual	0.27	≅ 0.23 (ns)	*Elymus nutans*	Sui et al. (2014)
Olax phyllanthi	shrub		0.45[6]	Natural community	Pate et al. (1990)
Castilleja miniata	perennial	0.28	< 0.37	*Lolium perenne*	Matthies (1997)
Castilleja chromosa	perennial	0.16	< 0.20	*Lolium perenne*	Matthies (1997)
Pedicularis canadensis	perennial		0.20- 0.30[4]	*Andropogon gerardii*	Borowicz and Armstrong (2012)
Annuals (mean ±1 SE)		0.15 ± 0.03	0.08 ± 0.02		
Perennials (mean ±1 SE)		0.24 ± 0.02	0.21 ± 0.03		
Shrubs and trees (mean ±1 SE)		0.61 ± 0.03	0.42 ± 0.03		

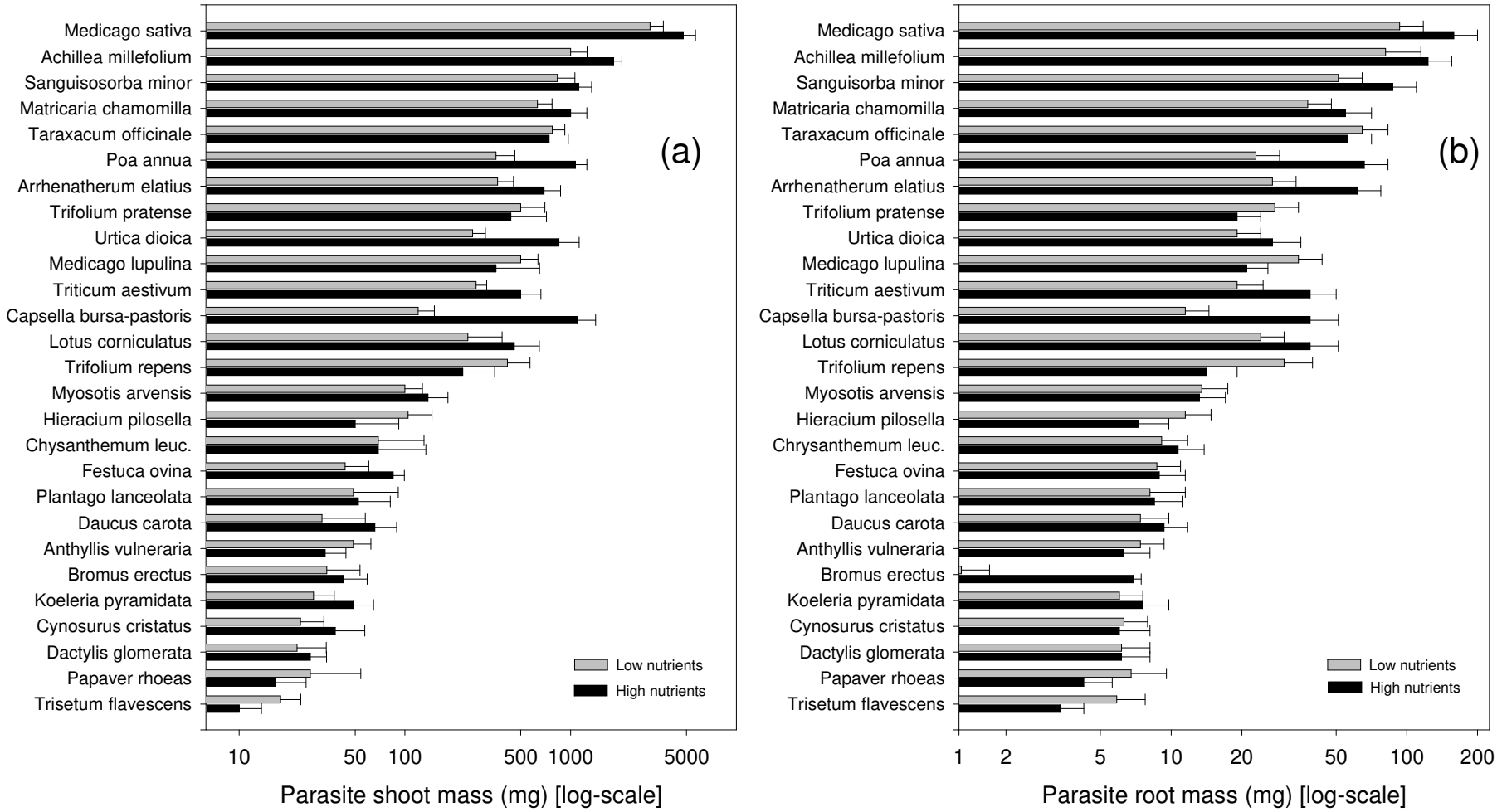
[1] Host killed after four weeks of growth; [2] depending on nutrient treatment [3] after only 14 days of growth [4] depending on nutrient and shade treatment, [5] depending on soil type [6] 3rd year plants

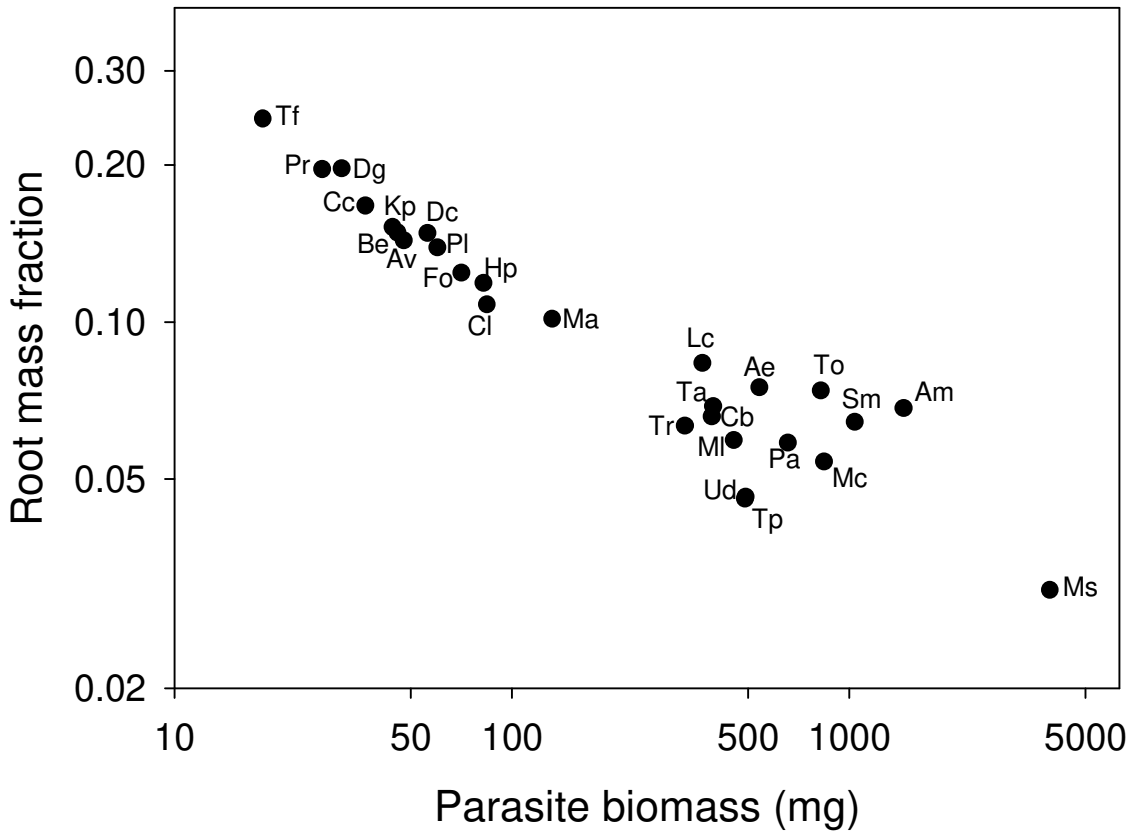
Table 7
The proportion of biomass allocated to roots (RMF) by various plant species that were grown on their own (-P) or in the presence of a root hemiparasite (+P). Host plants were marked as grasses (G), legumes (L), non-leguminous forbs (F) and trees (T). For results of the present study see Fig. 10. ns, effect of parasite not significant. However, not in all sources were statistical tests provided.

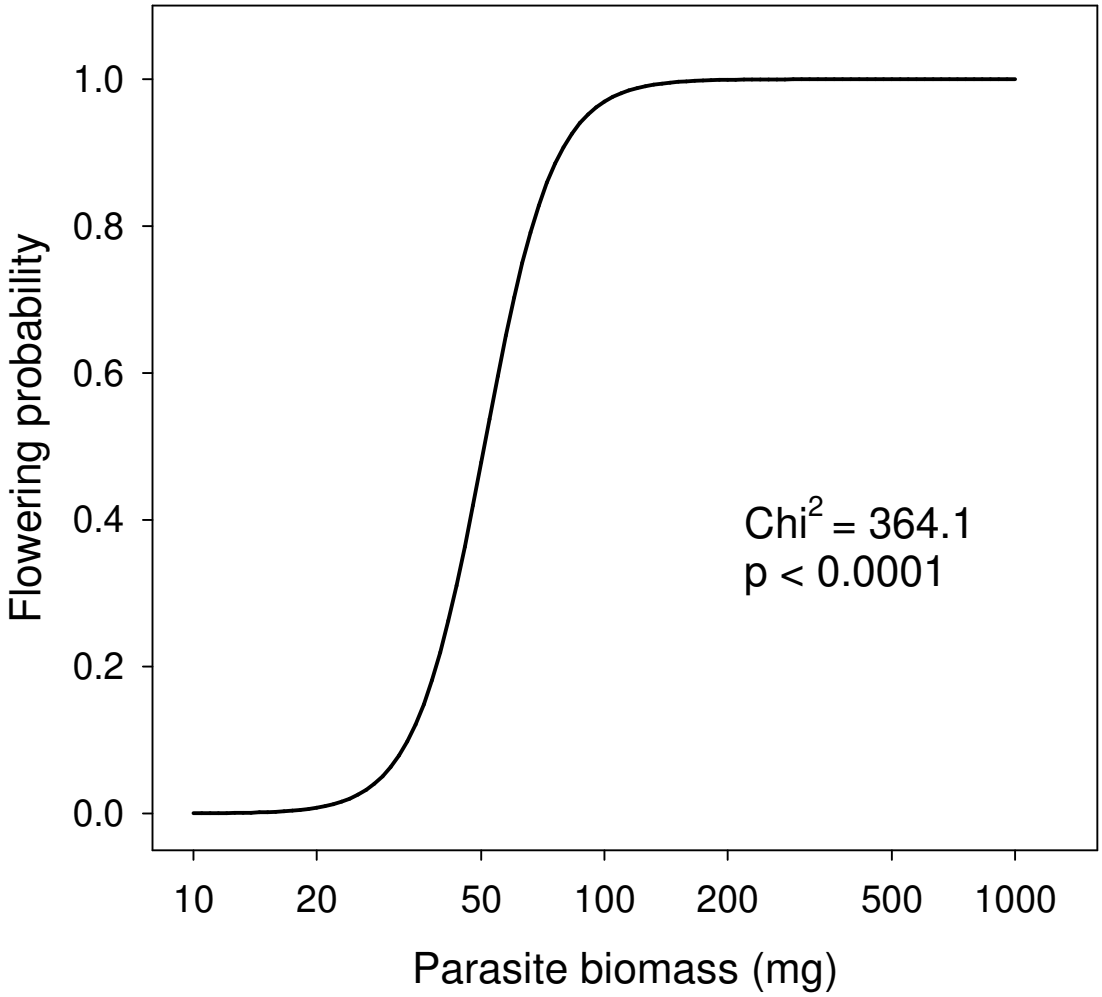
Host	Parasite	RMF -P		RMF +P	Source
Zea mays	*Striga hermonthica*	0.27	<	0.41	Aflakpui (2001)
Sorghum bicolor (G)	*Striga hermonthica*	0.22 / 0.17[1]	<	0.35 / 0.29	Parker (1984)
Zea mays var. 1 (G)	*Striga hermonthica*	0.24	<	0.49	Taylor et al. (1996)
Zea mays var. 2 (G)	*Striga hermonthica*	0.29	<	0.51	Taylor et al. (1996)
Zea mays var. 3 (G)	*Striga hermonthica*	0.21	<	0.49	Taylor et al. (1996)
Sorghum bicolor (G)	*Striga hermonthica*	0.56	<	0.76	Gurney et al. (2002)
Sorghum arundinaceum (G)	*Striga hermonthica*	0.61	<	0.75	Gurney et al. (2002)
Sorghum bicolor sensitive (G)	*Striga hermonthica*	0.22	<	0.43	van Ast et al. (2000)
Sorghum bicolor 38 d (G)	*Striga hermonthica*	0.15	<	0.28	Sinebo and Drennan (2001)
Sorghum bicolor 64 d (G)	*Striga hermonthica*	0.21	<	0.25	Sinebo and Drennan (2001)
Sorghum bicolor (G)	*Striga hermonthica*	0.17	<	0.53	Graves et al. (1989)
Pennisetum typhoides (G)	*Striga hermonthica*	0.12	<	0.43	Graves et al. (1990)
Sorghum bicolor (G)	*Striga hermonthica*	0.77	<	0.93	Watling and Press (1997)
Eragrostis pilosa (G)	*Striga hermonthica*	0.71	<	0.88	Watling and Press (1998)
Oryza sativa (G)	*Striga hermonthica*	0.26 - 0.35[1]	<	0.66 - 0.71[1]	Cechin and Press (1994)
Sorghum bicolor	*Striga hermonthica*	0.22 - 0.47[1]	<	0.25 - 0.69[1]	Cechin and Press (1993b)
Sorghum bicolor (G)	*Striga asiatica*	0.77	<	0.89	Watling and Press (1997)
Sorghum bicolor (G)	*Striga asiatica*	0.56	<	0.67	Gurney et al. (2012)
Vigna unguiculata (L)	*Striga gesneroides*	0.19	<	0.28	Graves et al. (1992)
Vigna unguiculata (L)	*Alectra vogelii*	0.37	<	0.75	Rambakudzibga et al. (2002)
Hordeum vulgare (G)	*Odontites verna*	0.11	<	0.18	Govier (1966)
Lolium perenne (G)	*Rhinanthus minor*	0.50	<	0.60	Graves (1995)
Leontodon hispidus (F)	*Rhinanthus minor*	0.24	<	0.28	Graves (1995)
Zea mays (G)	*Rhinanthus minor*	0.33 - 0.45[2]	<	0.45 - 0.56[2]	Těšitel et al. (2014)
Triticum aestivum (G)	*Rhinanthus minor*	0.37 - 0.56[2]	<	0.43 - 0.71[2]	Těšitel et al. (2014)
Lolium perenne (G)	*Castilleja miniata*	0.42	<	0.52	Matthies (1997)
Hordeum vulgare (G)	*Pedicularis rex*	0.32	<	0.34	Li et al. (2012a)

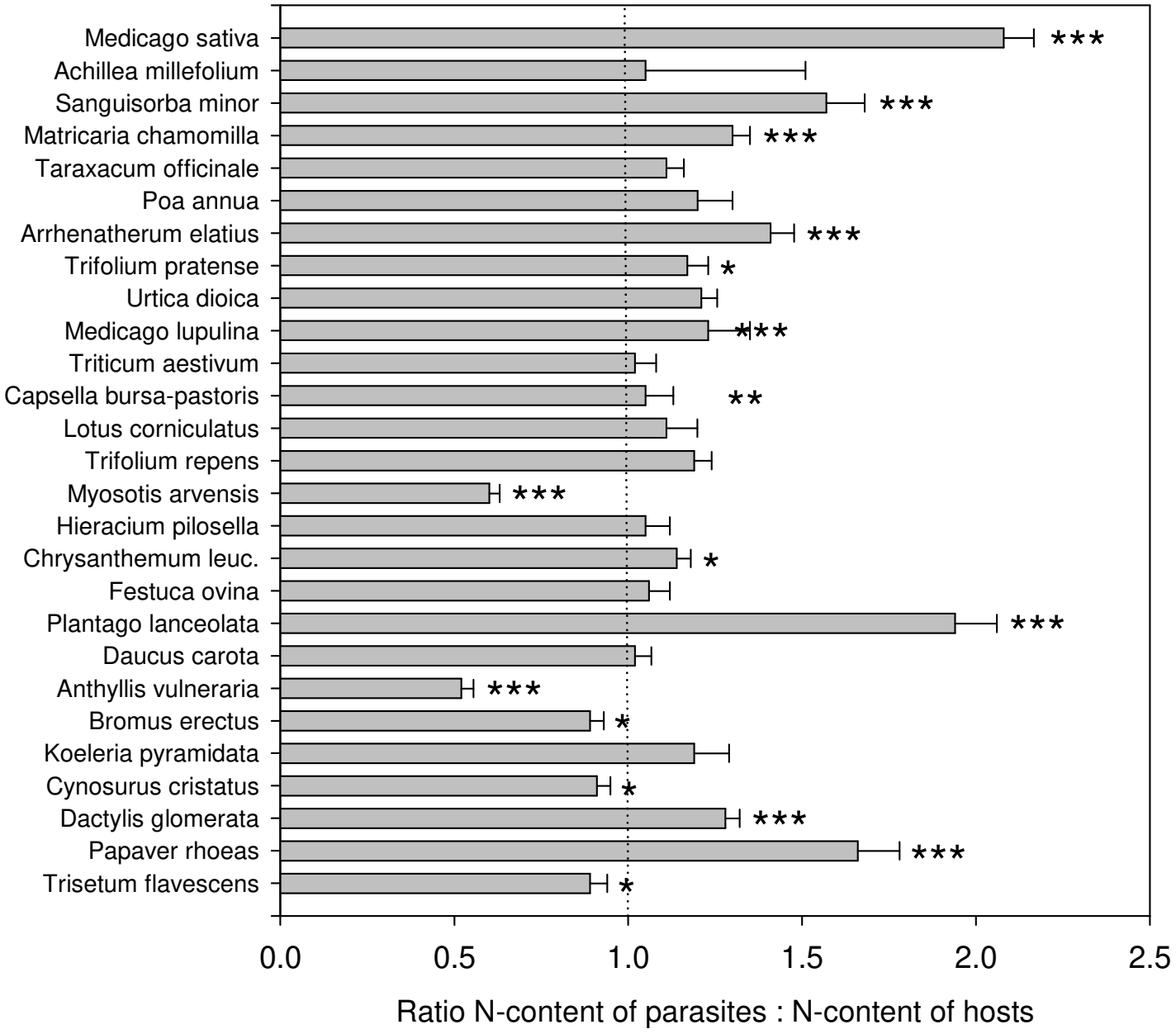
Hordeum vulgare (G)	*Pedicularis tricolor*	0.32	<	0.46	Li et al. (2012a)
Acacia littorea (T,L)	*Olax phyllanthi*	0.19	<	0.31	Tennakoon et al. (1997)
Agrostis capillaris (G)	*Rhinanthus serotinus*	0.65	≅	0.76 (ns)	Puustinen and Salonen (1999)
Agrostis capillaris (G)	*Rhinanthus serotinus*	0.50	≅	0.54 (ns)	Puustinen and Salonen (1999)
Sorghum arundinaceum (G)	*Striga asiatica*	0.61	≅	0.61 (ns)	Gurney et al. (2012)
Sorghum bicolor tolerant (G)	*Striga hermonthica*	0.36	≅	0.35 (ns)	van Ast et al. (2000)
Medicago sativa (L)	*Euphrasia minima*	0.38	≅	0.38 (ns)	Matthies (1998)
Lolium perenne (G)	*Euphrasia minima*	0.55	≅	0.52 (ns)	Matthies (1998)
Lolium perenne (G)	*Odontites vulgaris*	0.55	≅	0.54 (ns)	Matthies (1998)
Medicago truncatula (L)	*Pedicularis rex*	0.30	≅	0.36 (ns)	Li et al. (2012a)
Medicago truncatula (L)	*Pedicularis tricolor*	0.30	≅	0.38 (ns)	Li et al. (2012a)
Trifolium subterraneum (L)	*Pedicularis rex*	0.18	≅	0.32 (ns)	Li et al. (2012a)
Trifolium subterraneum (L)	*Pedicularis tricolor*	0.18	≅	0.24 (ns)	Li et al. (2012a)
Lolium perenne (G)	*Castilleja chromosa*	0.37	≅	0.43 (ns)	Matthies (1997)
Medicago sativa (L)	*Castilleja chromosa*	0.35	≅	0.37 (ns)	Matthies (1997)
Lolium perenne (G)	*Orthocarpus purpurascens*	0.37	≅	0.36 (ns)	Matthies (1997)
Medicago sativa (L)	*Orthocarpus purpurascens*	0.35	≅	0.38 (ns)	Matthies (1997)
Medicago sativa (L)	*Melampyrum arvense*	0.51	>	0.39	Matthies (1995b)
Medicago sativa (L)	*Odontites vulgaris*	0.38	>	0.29	Matthies (1998)
Medicago sativa (L)	*Odontites rubra*	0.50	>	0.40	Matthies (1995a)
Medicago sativa (L)	*Rhinanthus serotinus*	0.50	>	0.43	Matthies (1995a)
Medicago sativa (L)	*Castilleja miniata*	0.54	>	0.50	Matthies (1997)
Sesbania formosa (L)	*Santalum album*	0.61	>	0.49	Radomiljac et al. (1999)

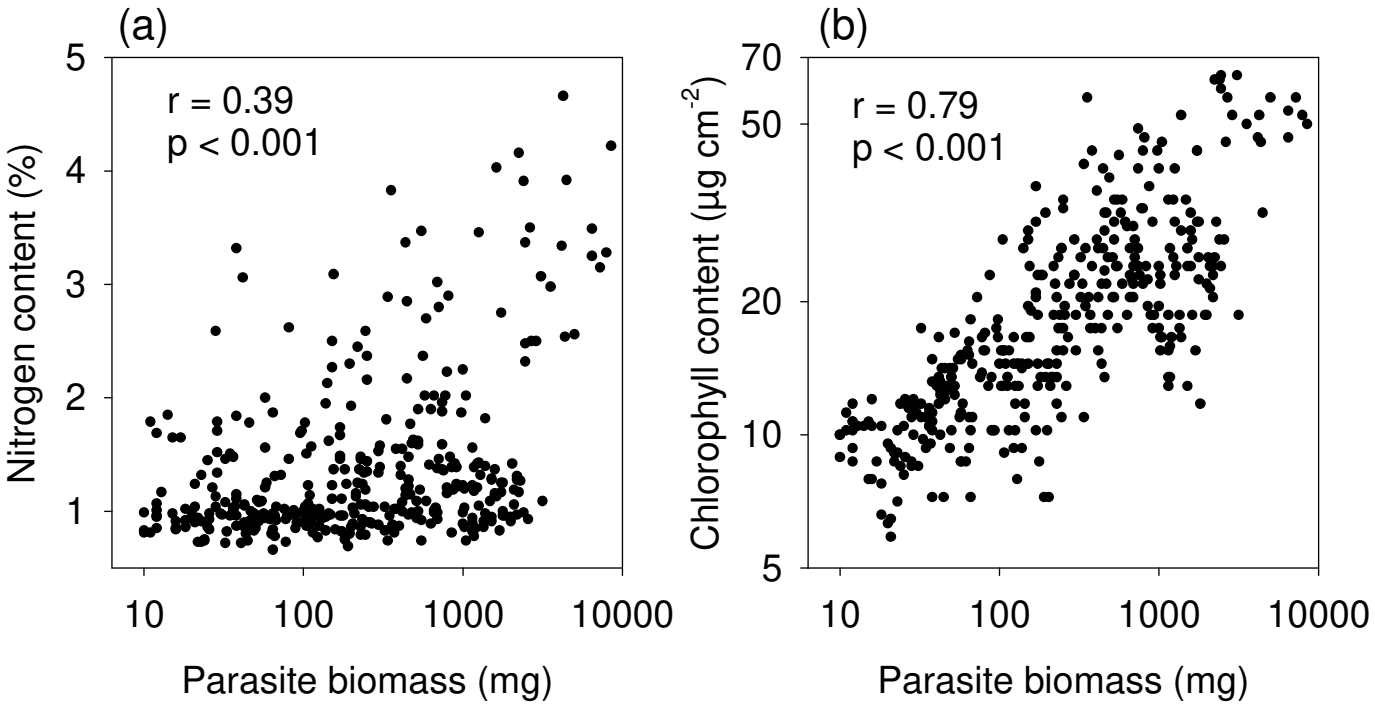
[1] Depending on nitrogen supply [2] Depending on nutrient and water supply

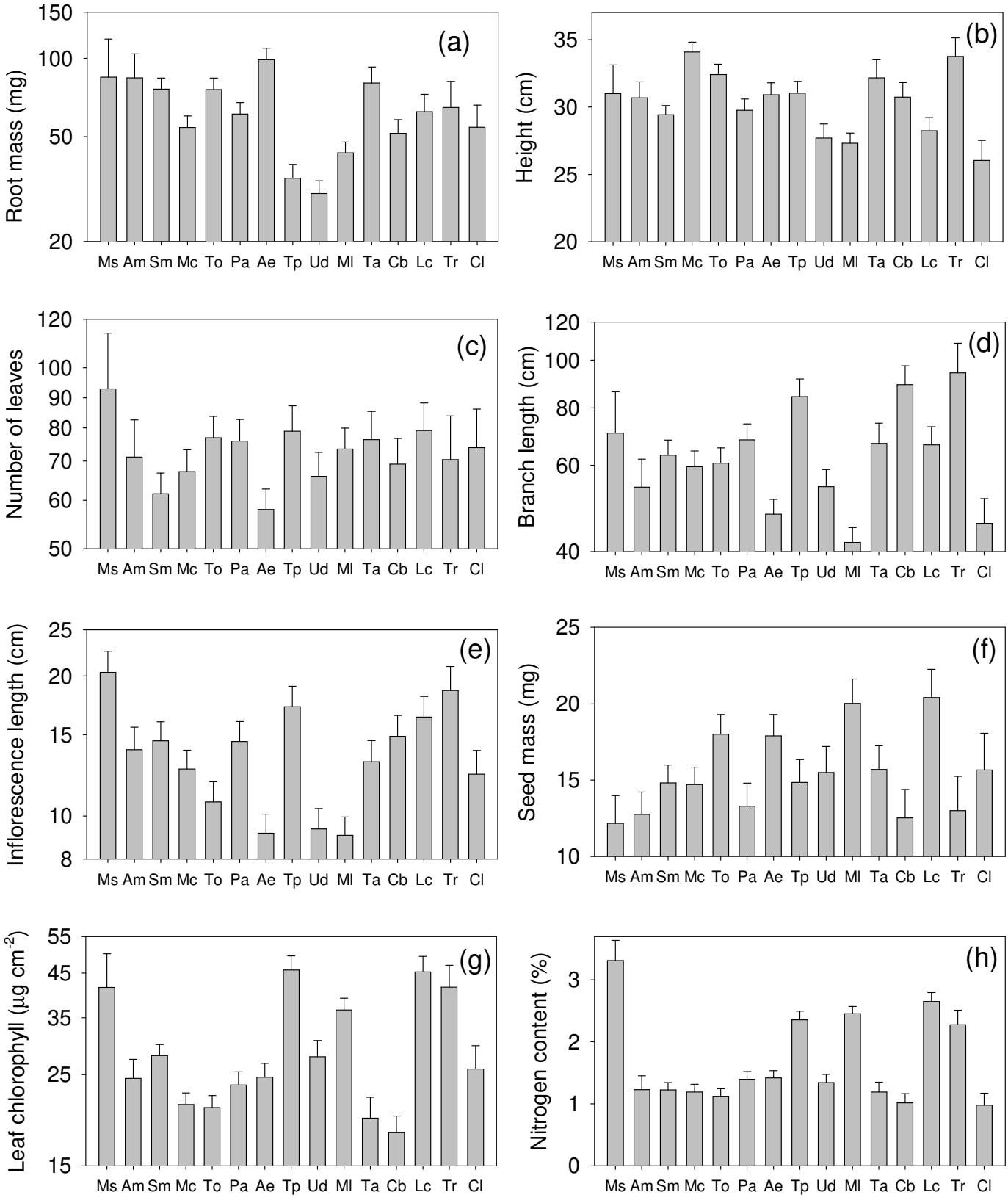

Medicago sativa
Achillea millefolium
Sanguisosorba minor
Matricaria chamomilla
Taraxacum officinale
Poa annua
Arrhenatherum elatius
Trifolium pratense
Urtica dioica
Medicago lupulina
Triticum aestivum
Capsella bursa-pastoris
Lotus corniculatus
Trifolium repens
Myosotis arvensis
Hieracium pilosella
Chysanthemum leuc.
Festuca ovina
Plantago lanceolata
Daucus carota
Anthyllis vulneraria
Bromus erectus
Koeleria pyramidata
Cynosurus cristatus
Dactylis glomerata
Papaver rhoeas
Trisetum flavescens
(a)
Low nutrients
High nutrients
10
50
100
500
1000
5000
Parasite shoot mass (mg) [log-scale]
Medicago sativa
Achillea millefolium
Sanguisorba minor
Matricaria chamomilla
Taraxacum officinale
Poa annua
Arrhenatherum elatius
Trifolium pratense
Urtica dioica
Medicago lupulina
Triticum aestivum
Capsella bursa-pastoris
Lotus corniculatus
Trifolium repens
Myosotis arvensis
Hieracium pilosella
Chrysanthemum leuc.
Festuca ovina
Plantago lanceolata
Daucus carota
Anthyllis vulneraria
Bromus erectus
Koeleria pyramidata
Cynosurus cristatus
Dactylis glomerata
Papaver rhoeas
Trisetum flavescens
(b)
Low nutrients
High nutrients
1
2
5
10
20
50
100
200
Parasite root mass (mg) [log-scale]

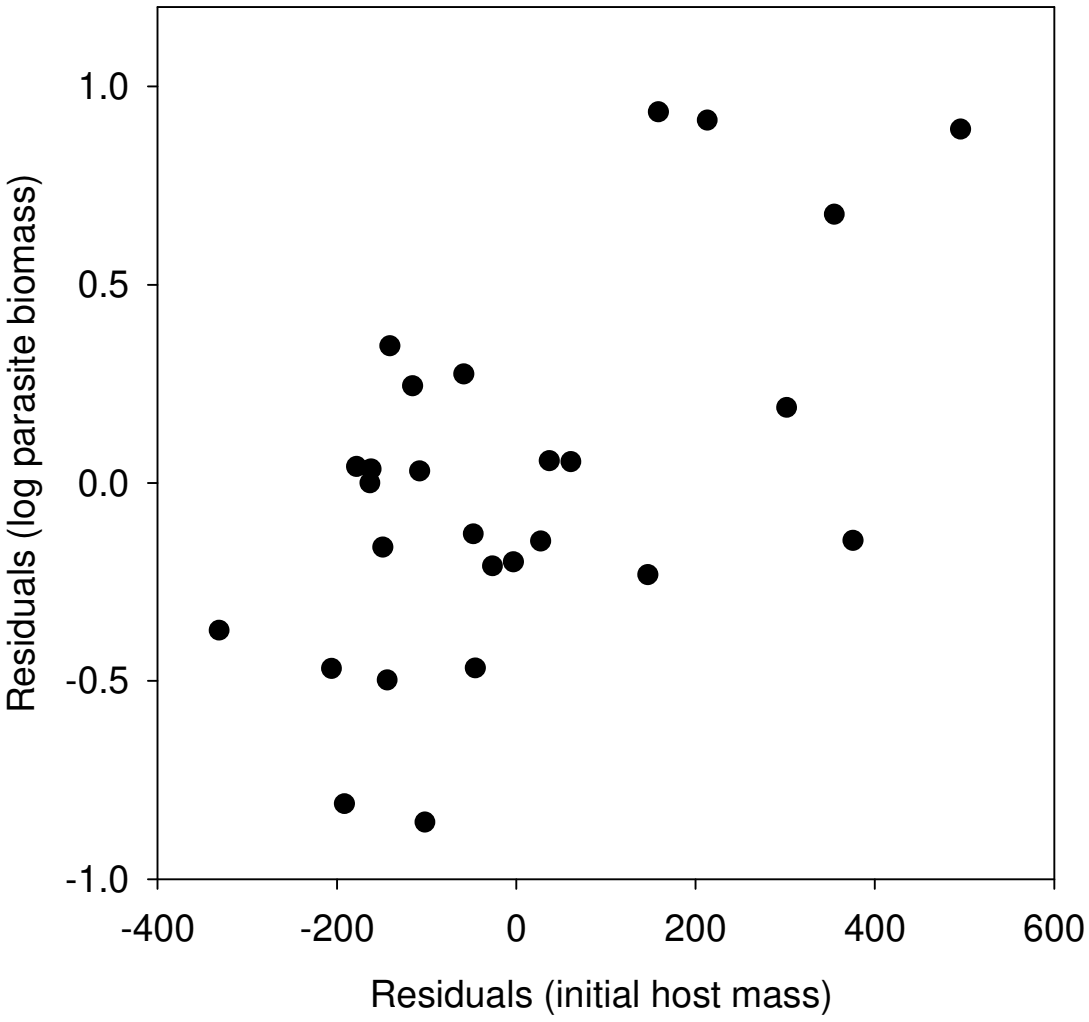

0.30
0.20
0.10
0.05
0.02
Root mass fraction
Tf
Pr
Dg
Cc
Kp
Dc
Be
Av
Pl
Fo
Hp
Cl
Ma
Lc
Ae
To
Ta
Sm
Am
Tr
Cb
Ml
Pa
Mc
Ud
Tp
Ms
10
50
100
500
1000
5000
Parasite biomass (mg)

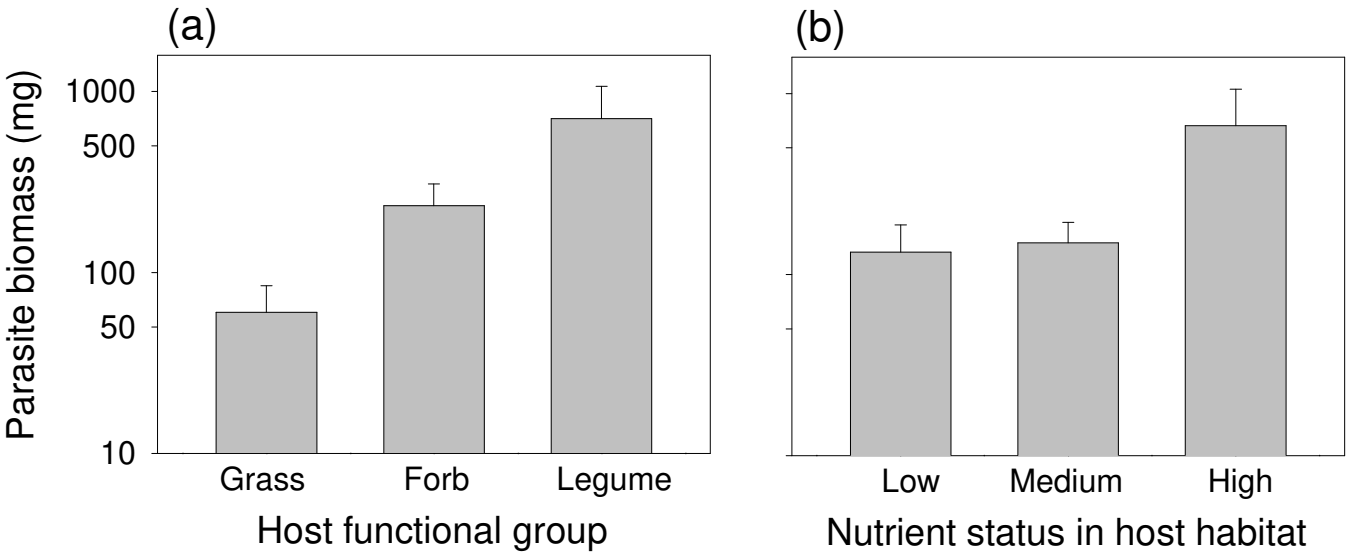

1.0
0.8
0.6
0.4
0.2
0.0
Flowering probability
Chi2 = 364.1
p < 0.0001
10
20
50
100
200
500
1000
Parasite biomass (mg)

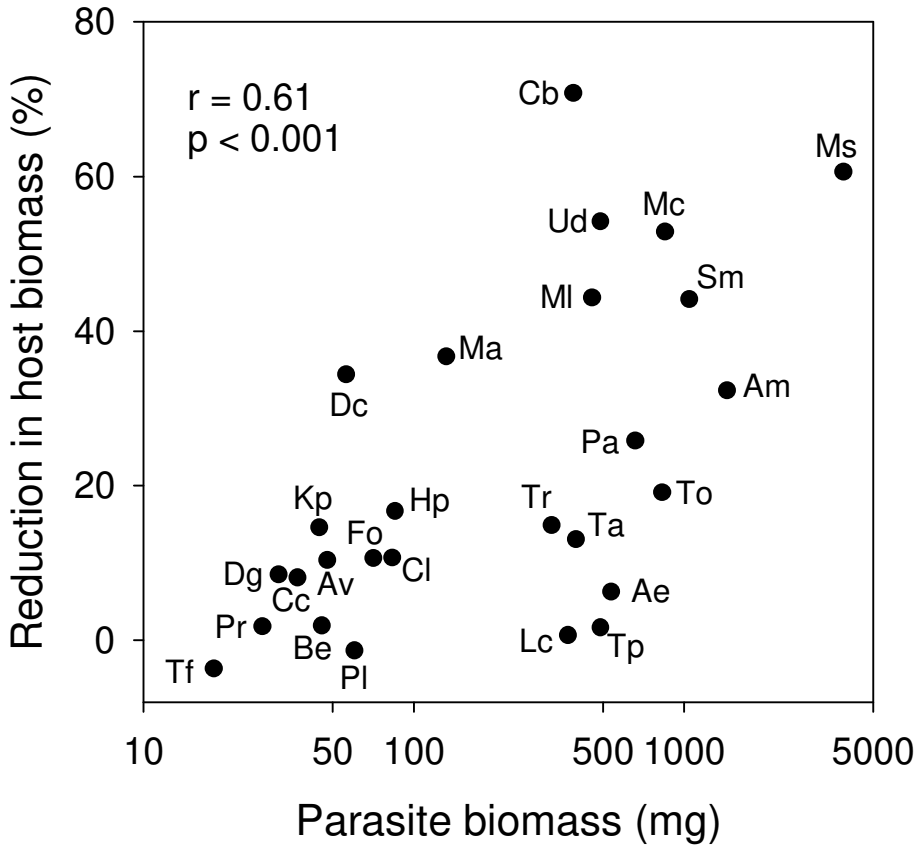

Medicago sativa ***
Achillea millefolium
Sanguisorba minor ***
Matricaria chamomilla ***
Taraxacum officinale
Poa annua
Arrhenatherum elatius ***
Trifolium pratense *
Urtica dioica
Medicago lupulina ***
Triticum aestivum
Capsella bursa-pastoris **
Lotus corniculatus
Trifolium repens
Myosotis arvensis ***
Hieracium pilosella
Chrysanthemum leuc. *
Festuca ovina
Plantago lanceolata ***
Daucus carota
Anthyllis vulneraria ***
Bromus erectus *
Koeleria pyramidata
Cynosurus cristatus *
Dactylis glomerata ***
Papaver rhoeas ***
Trisetum flavescens *
0.0
0.5
1.0
1.5
2.0
2.5
Ratio N-content of parasites : N-content of hosts

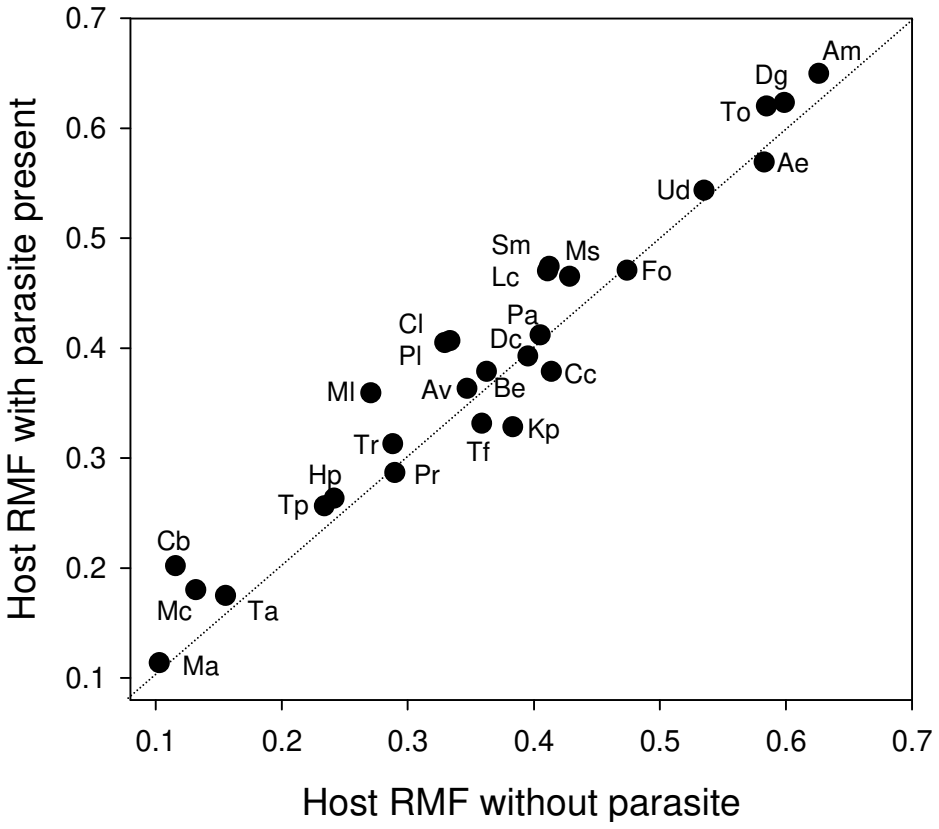

(a)
r = 0.39
p < 0.001
Nitrogen content (%)
5
4
3
2
1
10
100
1000
10000
Parasite biomass (mg)
(b)
r = 0.79
p < 0.001
Chlorophyll content (µg cm-2)
70
50
20
10
5
10
100
1000
10000
Parasite biomass (mg)

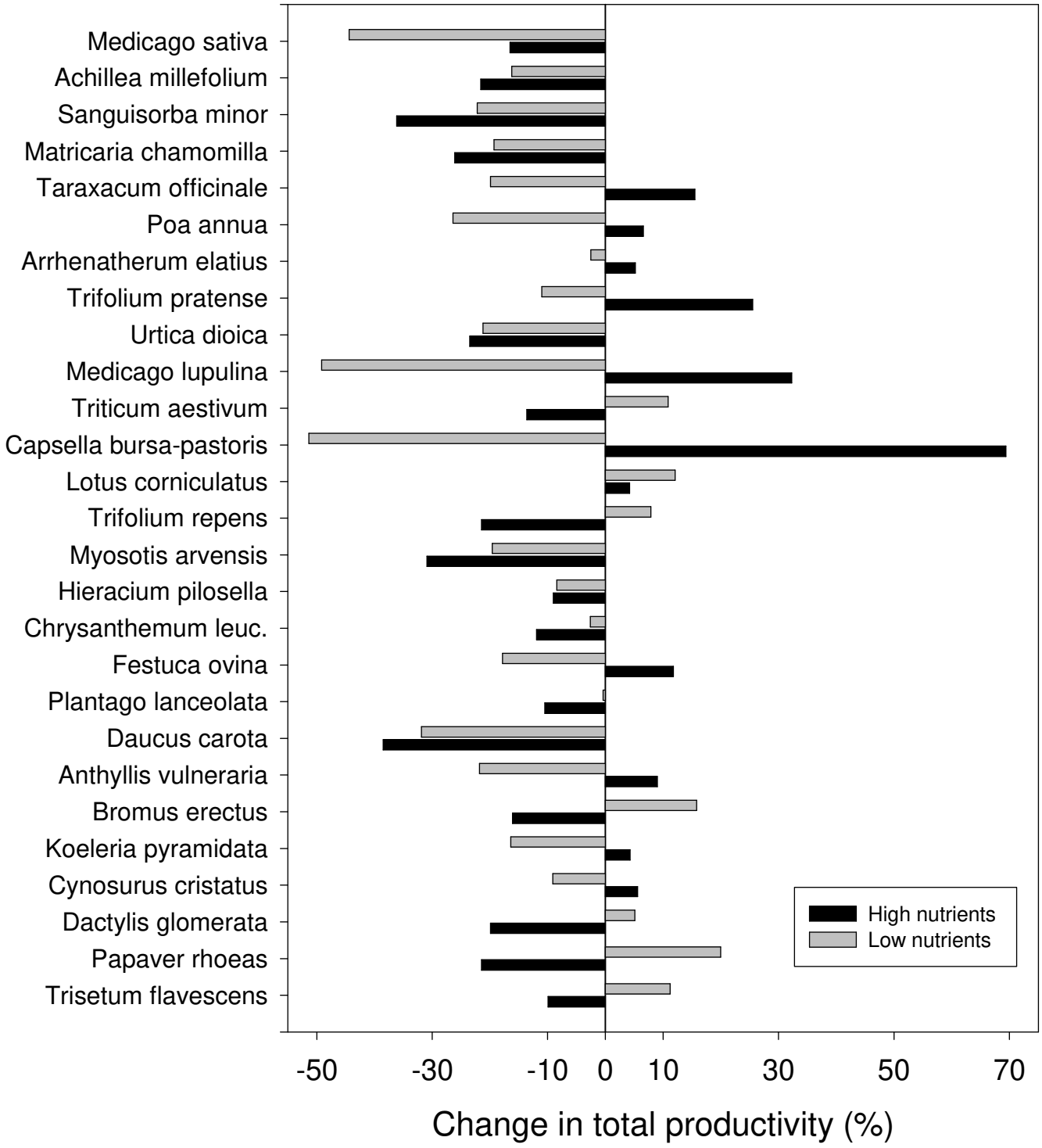

(a)
Root mass (mg)
150
100
50
20
(b)
Height (cm)
35
30
25
20
(c)
Number of leaves
120
100
90
80
70
60
50
(d)
Branch length (cm)
120
100
80
60
40
(e)
Inflorescence length (cm)
25
20
15
10
8
(f)
Seed mass (mg)
25
20
15
10
(g)
Leaf chlorophyll (μg cm-2)
55
45
35
25
15
(h)
Nitrogen content (%)
3
2
1
0
Ms Am Sm Mc To Pa Ae Tp Ud Ml Ta Cb Lc Tr Cl
Host species


1.0
0.5
0.0
-0.5
-1.0
Residuals (log parasite biomass)
-400
-200
0
200
400
600
Residuals (initial host mass)


(a)
Parasite biomass (mg)
1000
500
100
50
10
Grass
Forb
Legume
Host functional group
(b)
Low
Medium
High
Nutrient status in host habitat


r = 0.61
p < 0.001
Cb
Ms
Mc
Ud
Sm
Ml
Ma
Am
Dc
Pa
Kp
Hp
Tr
To
Fo
Ta
Dg
Cl
Av
Ae
Cc
Pr
Be
Lc
Tp
Tf
Pl
80
60
40
20
0
10
50
100
500
1000
5000
Reduction in host biomass (%)
Parasite biomass (mg)


Host RMF with parasite present
Host RMF without parasite
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Am
Dg
To
Ae
Ud
Sm
Ms
Lc
Fo
Cl
Pa
Pl
Dc
Cc
Ml
Av
Be
Kp
Tr
Tf
Hp
Pr
Tp
Cb
Mc
Ta
Ma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Plantago lanceolata
Daucus carota
Anthyllis vulneraria
Bromus erectus
Koeleria pyramidata
Cynosurus cristatus
Dactylis glomerata
Papaver rhoeas
Trisetum flavescens
High nutrients
Low nutrients
-50
-30
-10
0
10
30
50
70
Change in total productivity (%)